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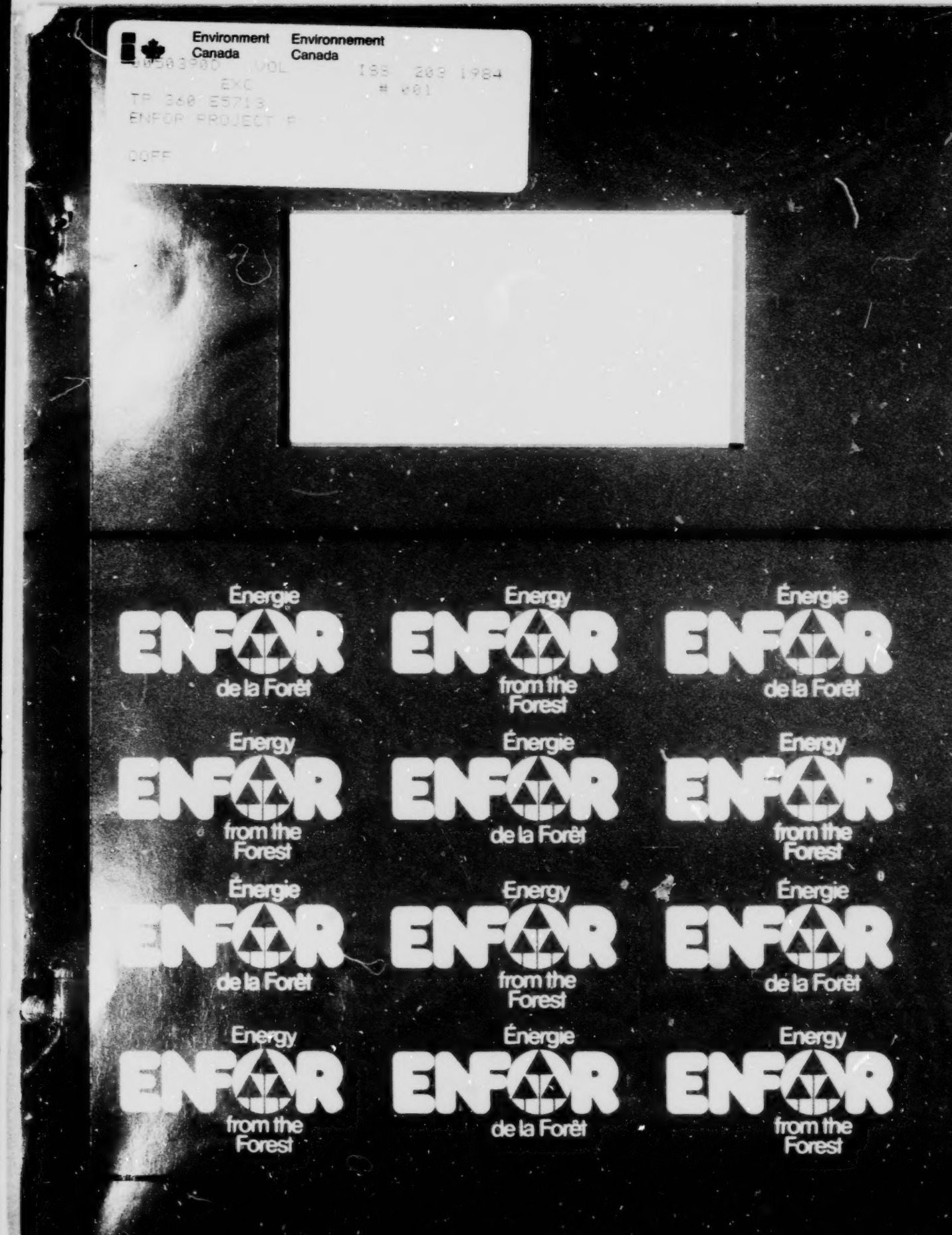

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ENFOR Project P-203

Impact on Wildlife of Short-Rotation Management of Boreal Aspen Stands

by

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ABSTRACT

A study was initiated in west-central Alberta in 1981 to determine the potential effects of short-rotation harvesting of boreal aspen stands on wildlife. The study involved a comparative evaluation of habitat conditions and wildlife use of aspen stands of different ages, including 1 and 2-year-old clearcuts and 14-, 30-, 60-, and 80-year-old stands. Changes in habitat structure between different successional stages resulted in a successional replacement of bird species with stand age. Overall densities of breeding birds would likely increase under short-rotation management, however approximately one-third of the species common to aspen forests would undergo a significant decrease in abundance. The absence of large diameter snags in managed stands would result in a pronounced decrease in abundance of snag-dependent birds. Browse production was highest in the 14-year-old stands while maximum production of grasses and forbs occurred in the 14- and 30-year-old stands respectively. As a result, short-rotation harvesting would be beneficial to ungulates as long as management programs include silvicultural options designed to meet the cover requirements of each species. Among the furbearing mammals, some species are expected to benefit while others would be adversely affected. Snowshoe hares, beaver, lynx, coyotes and wolves would likely benefit while species such as marten, fisher and red squirrel would be adversely affected by a reduction in the amount of aspen succeeding to mixedwood or coniferous forest under short-rotation management.

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1.0 INTRODUCTION

Utilizing the forest resource as a potential source of energy has recently received widespread interest in Canada. This interest has largely been a result of concerns over declining petroleum reserves and a commitment by the Canadian government to energy self-sufficiency. Consequently, a significant research and development effort was initiated by the Canadian Forestry Service under the auspicies of the ENFOR (Energy from the Forest) Program. The ENFOR Program will serve to inventory biomass production of Canadian forests, develop economically feasible harvesting and energy conversion technologies; and to evaluate and model potential environmental impacts of biomass harvesting.

Managing forests for biomass production has a high potential in Canada because almost 40% of the land base is comprised of forest cover (Carroll-Hatch Ltd. 1983). Although most of the productive forest land lies from Quebec westward (Brace and Croler 1982), the resource contributes significantly to the economy of all regions in the country (Carroll-Hatch Ltd. 1983). However, despite the economic importance and availability of forests in Canada, a significant portion of the forest land base remains untouched.

Recently, Young (1975, 1977) discussed the complete forest concept in relation to traditional forestry practices. Because only merchantable tree species and certain stem sizes are harvested during conventional harvesting operations, only 15% of the biomass produced on a site is utilized. In contrast, the complete forest concept is based on the complete removal of all vegetative matter from the site. The complete utilization of forest biomass may take the form of several alternate forest management strategies. These strategies have been reviewed by Telfer (1978) and include:

(a) complete utilization,
(b) production of native species on short-rotation,
(c) energy plantations, and
(d) large monocultures of exotics.

Production of native species on a short-rotation basis was the focus of the current investigation. This forest management strategy seeks to maximize biomass production in the shortest possible rotation. Therefore those

successional species that reproduce and grow rapidly on a wide range of site conditions are favored (Young 1977). Aspen is particularly well-suited for short-rotation management because it reproduces easily and quickly by suckering, exhibits rapid volume growth, attains maturity from 30-70 years and responds well to intensive management practices (Einsphar 1972). Bella and DeFranceschi (1980) have demonstrated that the mean annual volume increment is maximized at about 30 years of age, and that decay in aspen stands does not become prevalent until 70 years of age. In addition, aspen is one of the most common tree species in Canada. Recent estimates indicate that poplars (aspen, balsam poplar and black cottonwood) account for 54% (1.9 billion cubic meters) of the total hardwood resource and only 10% of the merchantable forest resource in Canada (Carroll and Hatch Ltd. 1983). Although the national annual allowable cut is approximately 42 million cubic meters, less than 5% of the poplar are harvested annually. In the prairie provinces, aspen often occurs in large pure stands. However, even though aspen accounts for approximately 30% of the merchantable wood resource on the prairies (Steneker 1976), it is presently being lightly utilized (Steneker 1976, Bella and DeFranceschi 1980).

The potential for converting aspen biomass to a usable supplemental energy source has raised serious concerns as to the possible impacts on wildlife during the harvest and post-harvest periods. Since biomass harvesting on a short-rotation basis would involve virtually complete utilization of the aspen stand at approximately 30 year intervals, substantial changes in the composition and relative abundance of wildlife species can be expected. The possible implications to wildlife of harvesting aspen on a short-rotation basis (30 years) were assessed during the present study under the ENFOR Program (P-203). The overall objective of the study was to assess habitat quality and use by wildlife in differently aged aspen stands. Specific objectives included:

(a) assess and compare habitat conditions of one-year-old clearcuts, 14-, 30-, 60- and 80-year-old aspen stands.

(b) determine the species composition and relative abundance of ungulates, snowshoe hare and avifauna in the differently aged aspen stands.

(c) identify habitat components which will be affected by the implementation of a 30-year harvest rotation of aspen stands,

(d) identify and evaluate wildlife losses and gains in relation to a 30-year harvest rotation.

2.0 METHODS

2.1 STUDY AREA

The study area is situated in the vicinity of Medicine Lake, approximately 35 km north of Rocky Mountain House, Alberta (Figure 1). The Medicine Lake area is located in the Lower Foothills section of the Boreal Forest Region (Rowe 1972), and is characterized by extensive stands of aspen, balsam poplar and lodgepole pine. These stands are of fire origin but if left undisturbed, they will proceed to mature stands of climax white spruce. White birch tends to occur on upland sites within the study area, while black spruce and tamarack dominate the depressional areas (Rowe 1972).

The Medicine Lake study area is situated in the Western Alberta Plains physiographic unit, and is underlain by gently undulating Cretaceous and Tertiary bedrock (Atlas of Alberta 1969). The surficial deposits in the area are characterized by hummocky or rolling till moraines. Topography of the area is described as rolling, with some plateaus interspersed among low and high rounded hills which range in elevation from 900 to 1200 m (Rowe 1972). Gray Luvisolic soils are common on upland sites in the area while Gleyed Luvisols and Gleysols are found in the imperfectly drained sites (Strong and Leggat 1981). Poorly drained areas are typically characterized as depressional and are overlain by organic deposits of varying depths.

Meteorological information from Rocky Mountain House indicates an annual mean daily temperature of 2.6°C, however mean daily temperatures range from -13.0°C in January to 15.4°C in July (Atmospheric Environment Service 1973). Annual winter and summer precipitation values are 377.6 mm and 177.1 mm, respectively. The average number of frost-free days in the Rocky Mountain House area is 80 days.

2.2 APPROACH AND STUDY DESIGN

Study grids were established in aspen stands representing five age classes. Efforts were made to select stands that were comparable with respect to topography, aspect, distance from roads and other possible disturbance factors, however the nature of the terrain in the foothills region made standardization of

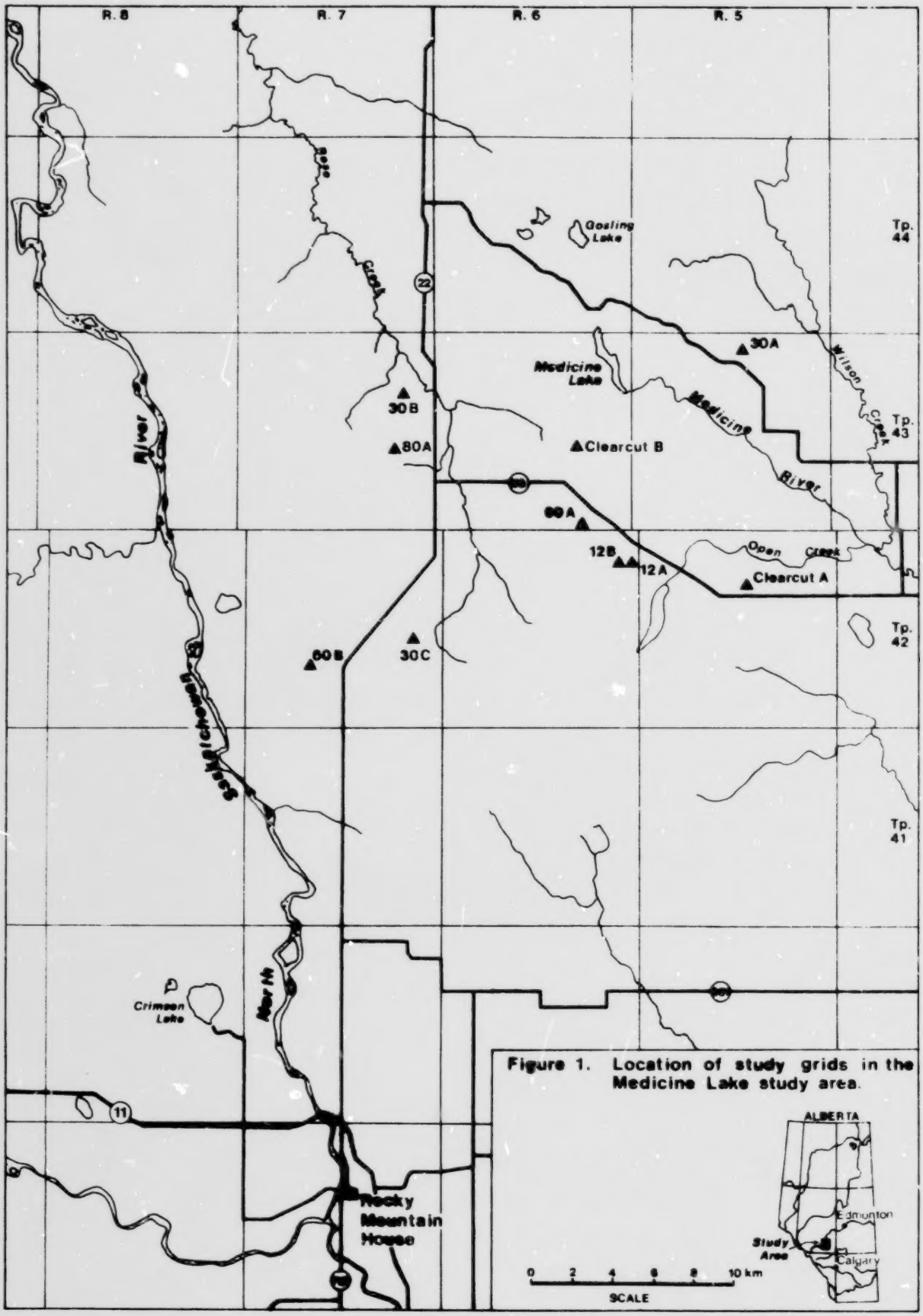


Figure 1. Location of study grids in the Medicine Lake study area.

site conditions difficult. Ten study sites representing five age classes were selected within a 360 sq km area (Figure 1). These sites included clearcut (0-3 years), 14, 30 (30-33 years), 60 (60-63 years) and 80 (80 years plus) years.

A rectangular sampling grid was established at each of the sample sites. Transects were systematically placed at 50 m intervals, along pre-determined compass bearings. Permanent sample points were then established at 25 m intervals along each transect. These points served as centers for subsequent measurement of habitat characteristics and wildlife use. The use of a systematic sampling approach ensured that a representative sample of vegetation and wildlife use was obtained in relation to variations in topography, and also facilitated efficient relocation of sample points in dense vegetation.

Grids established prior to 1982 (clearcut, 14-, 30- and 60-year-old) were renamed as Clearcut A, 14A, 30A and 60A grids. The six new grids (referred to as Clearcut B, 14B, 30B, 30C, 60B and 80A) were surveyed and marked in May 1982. New grids 30B, 30C, 60B and 80A were similar in size and shape to grids 30A and 60A (Table 1). These rectangular grids measured 250 m wide by 475 m long and occupied 11.9 ha. Grid 14B was similar to Plot 14A in width (250 m) but was 25 m longer (275 m). Clearcut B measured 250 m by 275 m and was smaller than Clearcut A (350 m by 300 m). Both clearcut grids included some of the surrounding forest. Clearcut A contained 104 sample points, 68 of which were located in the 60-year-old forest in 1981. Only 21 sample points remained in the 60-year-old forest after further clearing in 1982. Clearcut B had 66 sample points of which 37 were located in the surrounding 30-year-old forest.

2.3 HABITAT COMPOSITION

An initial inventory of forest stand composition was conducted on the three study plots established during the 1981 field season. Measurements of tree height (m), diameter at breast height (dbh-cm), canopy thickness (m), crown shape and crown radius were taken in sample plots placed at randomly selected grid locations. Fifteen, 100 sq m plots were sampled in the 30- and 60-year-old stands and 25, 25 sq m plots were sampled in the 14-year-old stand. Crown volume was determined using procedures described by Mawson et al. (1976). Basal areas were measured at 50 stations on each grid with a BAF 10 wedge prism.

Table 1. Numbers of transects and grid intersects by study grid in the Medicine Lake study area.

Study Grid	No. of Transects	No. of Plots	Area (ha)
Clearcut A	8	104	10.5
Clearcut B	6	66	6.9
14A	6	66	6.3
14B	6	72	6.9
30A	6	120	11.9
30B	6	120	11.9
30C	6	120	11.9
60A	6	120	11.9
60B	6	120	11.9
80A	6	120	11.9

During the 1982 field season, a detailed habitat description was prepared at each grid intersect for all 10 study grids. This was done in conjunction with breeding bird surveys and was designed to permit the analysis of: (a) the habitat features of an aspen forest which change over time, and (b) the relationship between songbirds and these habitat features.

Thirty-four habitat variables were evaluated at each grid intersect of all study sites. While the evaluation was based on an area within 10 m of the grid point, the description was assumed to be descriptive of a 25 m by 50 m block centered at the grid intersect. Total canopy cover was measured as the percentage of the sky obscured by tree leaves. Stems greater than 5 m in height were considered as part of the canopy layer. Proportions (%) of the total canopy cover value were then estimated for aspen, balsam poplar, white birch and conifers. Total cover for tall shrubs was similarly estimated for aspen, balsam poplar, white birch, willow, green alder and conifers. Tall shrubs were defined as stems ranging from 2.5 m to 5 m in height. Estimates of low shrub cover (%) were partitioned into the following categories: aspen, balsam poplar, white birch, willow, green alder, low-bush cranberry, rose, bracted honeysuckle and other low shrub species. Stems between 0.5 and 2.5 m in height were considered as low shrubs. Cover values were also applied to categories of bare soil, leaf litter, standing water, grasses (monocots), other flowering plants (dicots), horsetails, mosses and lichens. These values were obtained by estimating the percentage of ground covered by each category. Canopy height was defined as the distance from the ground to the top of an average tree while canopy depth was considered as the height from the top of an average tree to the bottom of the canopy.

The relative abundance of snags was assessed for each of the study grids. Snags were defined as any dead or partly dead tree at least 1 m tall. This definition was designed to include all snags which not only had the potential for cavity nesting but could also provide a foraging substrate for various bird species. The following characteristics were recorded for each snag encountered within the six, 2 m by 250 m belt transects established at each study grid: (a) snag condition (hard or soft), (b) mortality factor, (c) percentage of limbs that have been broken, and (d) percentage of bark remaining. Any signs of cavity nesting or feeding by birds or other groups of wildlife were also noted.

A deadfall survey on each study grid was conducted in conjunction with the snag survey. All deadfall intercepting a line transect were classified according to two size classes: (a) small (less than or equal to 10 cm in diameter), (b) large (greater than 10 cm in diameter). Additional information regarding species, height above ground (cm), diameter (cm) at the point of line interception, condition class and wildlife use were recorded for all large pieces of deadfall.

Data on forb and leaf biomass were collected in July 1981. Twenty-five 0.25 sq m circular plots were placed in each of the five study grids sampled in 1981. All forbs, grasses and short woody shrubs less than 0.5 m in height were clipped at ground level and were sorted according to species. The samples were then dried and weighed to the nearest 0.01 gm.

Shrub and sapling (stems less than 2.5 cm dbh) densities of the 10 study grids were determined during the summer of 1982, using the corrected-point-distance method (Batchelor 1973). At each grid intersect, a distance was measured from the flagged sample point to the nearest stem, then a second distance to that stem's nearest neighbor was measured and finally a third distance was recorded to its nearest neighbor. The following information was recorded for each stem measured: species, number of stems per clump and height (m). Data were analyzed using a FORTRAN computer program supplied by Dr. J. Smith (CWS, Vancouver, B.C.).

Differences in habitat composition among the forest age classes were evaluated using analysis of variance (ANOVA) procedures. Seven vegetation cover variables were analyzed. These included total canopy cover (%), total tall shrub cover (%), total low shrub cover (%), canopy height (m), canopy depth (m), total vegetative cover (%), and ground cover (%). Ground cover was defined as the combined cover values of the monocot and dicot categories. Snag variables and forb, grass and short woody shrubs were also examined for differences among forest age classes using a series of one-way ANOVA's.

Because of non-normal distributions and unequal variances, all percentage variables were transformed using the arcsine transformation prior to ANOVA (Kleinbaum and Kupper 1978, Sokal and Rohlf 1981). All other variables required a common logarithmic transformation. Statistically significant differences disclosed by ANOVA were partitioned by the Modified Least Significant Difference (MODLSD) multiple comparison procedure (SPSS Inc. 1983).

2.4 AVIFAUNA SURVEYS

Winter bird surveys were conducted following the establishment of study grids 14A, 30A and 60A in January 1981. Each study grid was censused eight times between 22 January and 5 March 1981. All birds seen or heard within 25 m of each transect were recorded. The number of birds recorded were averaged to obtain densities on a species basis for each study grid.

Breeding bird surveys were conducted on four study grids in 1981 using the territory mapping (spot-mapping) technique (Williams 1936). Surveys were repeated in 1982 on the same four plots as well as on the six new grids. Breeding bird surveys were conducted from 25 May to 25 June between 0500 and 0900 hr. Grid maps of observations prepared at each grid visit were copied to grid maps for each bird species. Information accumulated on each bird species was interpreted in terms of recognizable territories. A species sighting had to have been recorded on at least three days, or concurrent songs with an additional record on another day had to be recorded before a territory was defined. A nest was also sufficient evidence of a territory. A scatter of many observations throughout a grid was interpreted as one territory. Territories spanning a grid boundary were counted as half territories if at least one-half of the territory was located within the grid. The bird species maps were also interpreted in terms of the presence or absence of each species in the 25 m by 50 m blocks centered at each grid intersect. Species diversity indices for each age class were calculated using the Shannon formula: $H' = -\Sigma P_i \log P_i$.

Where H' is diversity and P_i is the proportion of observations in the ith species ($i = 1$) (Shannon 1948).

Pearson correlation coefficients were generated for all pairwise combinations of the 32 originally measured habitat variables. Those variables that were significantly correlated ($r = 0.70$, $P < 0.05$) were omitted from subsequent multivariate analyses. Therefore, only 10 uncorrelated habitat variables were used. These variables included total canopy cover, total tall shrub cover, total low shrub cover, ground cover, canopy height, canopy depth, total vegetation cover and volume index. Total vegetation cover was calculated as the sum total of all cover variables, while the volume index represented the product of canopy depth and total canopy cover. The data set used in examining bird species-habitat

relationships was comprised of a 10 x 31 (habitat variables x bird species) data matrix. Average values for each habitat variable were obtained by selecting only those grid intersects which contained two or more sightings for each bird species. This criterion assumed that two or more sightings of a species would reflect its preferred habitat.

The investigation and analysis of bird distribution with respect to specific habitat features was based on multivariate statistical procedures. Multivariate techniques permit the simultaneous analysis of individually measured habitat variables and of all bird species encountered on the study grids. Principal components analysis and cluster analysis, which are two widely used multivariate procedures in avian habitat studies (Anderson 1979, Mauer et al. 1981), were used in the present study.

Principal component analysis (PCA) is often used to simplify and describe species-habitat relationships by reducing the dimensionality of the data set. A new set of orthogonal and uncorrelated composite variates are formed by linearly combining the original set of variables such that each successive composite variate accounts for a smaller portion of the total variation in the data set (Berenson et al. 1983). Therefore, the first component will account for the largest amount of variation and the second will account for less than the first component but more than the third and so on. Cluster analysis is generally a classificatory procedure which functions to subdivide or partition a set of heterogeneous objects into relatively homogeneous groups (Berenson et al. 1983). That is, the overall objective of cluster analysis is to maximize dissimilarities between groups while at the same time minimizing within group dissimilarities.

In the context of the present study, PCA was used to derive a set of common component habitat variables which best described the variation in bird species distributions in the study area. A varimax rotation of the principal components was used to improve the interpretability of the component scores. PCA was performed using the FACTOR procedure of the SPSS program package (SPSS Inc. 1983). The resulting component scores for each individual bird species were then used as the input data matrix for cluster analysis. Cluster analysis was used to examine individual bird species relationships and to define bird species affiliations (associations) with respect to the PCA scores. Because there are numerous

clustering algorithms currently available, a method was selected by examining a comparative review of numerical classification methods by Frenkel and Harrison (1974). On this basis, classification of individual bird species into avian associations was accomplished using Ward's hierarchical clustering procedure of the CLUSTAN 1C computer program package (Wishart 1978). Ward's method is polythetic and agglomerative and has been described as possibly the best of the hierarchical options available (Wishart 1978). The similarity coefficient which exhibited the largest change in relative magnitude was used as the significant cluster level (Frenkel and Harrison 1974).

2.4 BROWSE SURVEYS AND PELLET GROUP COUNTS

Data on available browse biomass were collected for each study grid at the start of the winter browsing period. The current annual growth (CAG) of 60 twigs of each species found within each study grid was collected. Attempts were made to clip two twigs from the bottom, middle and top thirds of each plant sampled. This material was subsequently oven dried for 48 h at 70°C (Telfer 1972) and weighed to the nearest 0.01 gm. Browse production per ha was calculated as the product of the density of stems per ha, the mean number of twigs per stem and the mean twig weight for each species.

Browse surveys were conducted following the winter browsing period to determine the amount of browse removed from the tagged sample stems. The number of browsed twigs and unbrowsed twigs remaining on each stem was recorded along with the diameter of browsed twigs at the point of browsing (DPB). The biomass of browse utilized by ungulates was determined by relating the mean DPB to weight-diameter regression equations developed for each browse species. These equations were developed by drying and weighing tagged twigs of measured diameter collected during the fall sampling program. Since browse utilization sometimes exceeds the current annual growth, diameter-weight measurements were extended to include older growth.

Since some species of herbivores, particularly moose, rely heavily on leaves for forage during spring and summer, an effort was made to quantify the amount of leaf biomass available in aspen stands of different ages. At each sample point, the leaves were stripped from the nearest stem (greater or equal to 0.5 m in

height) of each shrub species to a height of 2.5 m. The leaf samples were identified to species, dried and weighed to the nearest 0.01 g. Available leaf biomass for each study grid was calculated as the product of the mean weight of leaves per stem and the density of each shrub species.

Pellet group counts were conducted in conjunction with the spring browse surveys. Ungulate pellet groups were counted on 100 sq m circular plots centered at each of the grid intersection points. Plots were reduced to 50 sq m on the 14-year-old plots because of dense vegetation and large amounts of deadfall. Hare pellets were counted in 1 sq m quadrats located at each grid intersection point. Pellet group counts were conducted on the 14-, 30- and 60-year-old study grids in 1981 and on all 10 study grids in 1982.

Statistical procedures for browse utilization by ungulates and snowshoe hares followed Neu et al. (1974). The chi-square statistic was used to test the null hypothesis that ungulates and snowshoe hares utilized browse species in proportion to their availability. If the null hypothesis was rejected a Bonferroni Z statistic was calculated to determine browse species preference or avoidance. Regression equations in the form: $\log_{10} Y = a + b (\log_{10} X)$ were developed from the weight-diameter measurements. These equations were then used for determining the amount of browse utilized by ungulates in the Medicine Lake study area.

A series of one way ANOVA's was used to examine ungulate and snowshoe hare use of the five forest age classes. The analysis was based on the mean number of pellet groups per plot for each ungulate species (or mean pellets for snowshoe hares). Data were transformed prior to ANOVA, using a square root ($\sqrt{x + 0.5}$) transformation. Square root transformations are particularly appropriate for count data exhibiting Poisson distributions (Sokal and Rohlf 1981). The addition of a constant (0.5) to each data point was used to reduce the number of zero values which are generally numerous when count methods are employed. Significant differences identified during ANOVA were partitioned using Fishers Significant Difference (FSD) multiple comparison procedure (Kleinbaum and Kupper 1978)

3.0 RESULTS

3.1 STUDY GRID DESCRIPTIONS

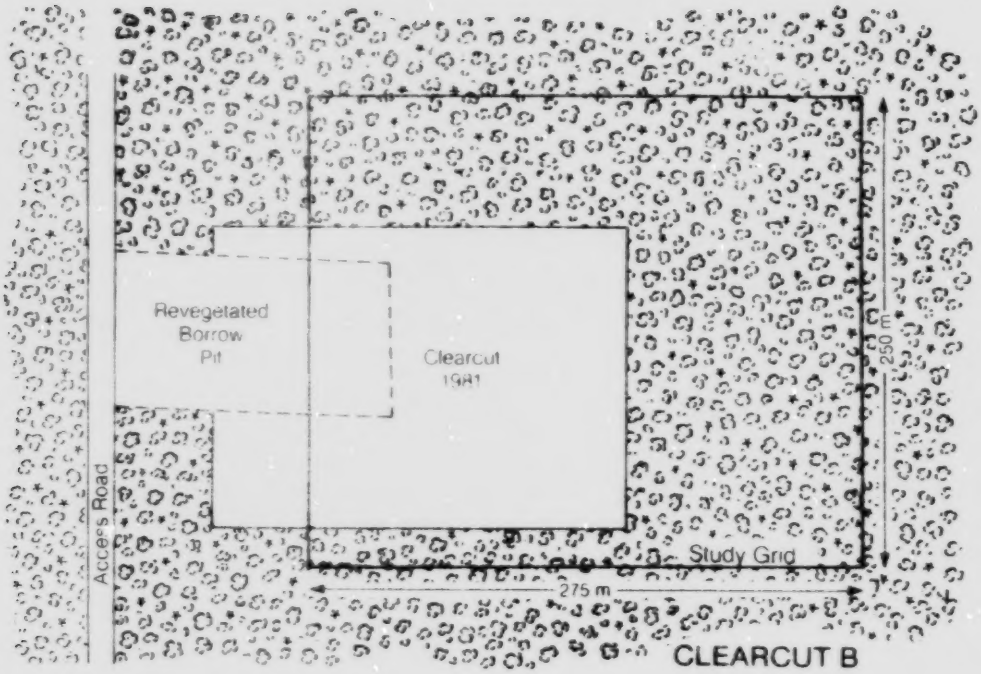
Sixteen species of trees and shrubs (Appendix I) and 64 species of forbs, grasses and short woody shrubs (Appendix II) were identified in the Medicine Lake study area. Biomass estimates for forbs, grasses and short woody shrubs are summarized in Appendices III and IV. Mean values for the habitat characteristics measured on the 10 study grids are presented in Appendix V.

3.1.1 Clearcut A Grid

The Clearcut A Grid which was surveyed and marked in May 1981, was a clearcut of a 60-year-old aspen stand. This clearcut was established by the Canadian Forestry Service during an aspen harvesting study being conducted as part of the ENFOR program. The study grid extended into the surrounding forest on the north, west and south sides, while the east side was contiguous with the forest edge (Figure 2). During the winter of 1981-82, extensive areas were cleared of trees for a grazing lease. This meant that the forest remained intact only along the south side of the plot; a 100 by 100 m block of trees remained in the northwest corner of the plot; and cleared land extended from the west, north and east sides of the plot. Hence, the habitat descriptions prepared during the summer of 1982 apply only to that year for Clearcut A.

Forested portions of Clearcut A had a canopy height of 16.1 m and a canopy depth of 7.5 m. Total canopy cover in the forested portion of Clearcut A was relatively open with aspen dominating the canopy. Balsam poplar and some white birch were also present. Green alder was the dominant tall shrub and accounted for about three-quarters (16.5%) of the total tall shrub cover. Cover provided by the low shrub layer was less than that on most plots. Standing water was found in the northwest corner of the plot in May and June but had dried up by July.

The clearcut portion of the grid had no canopy cover, and the tall shrub layer was essentially absent. Portions of the grid which were cleared prior to spring 1981, had a luxurious suckering growth of aspen, balsam poplar, willow and green alder. Portions which were cleared during the 1981-82 winter had not yet



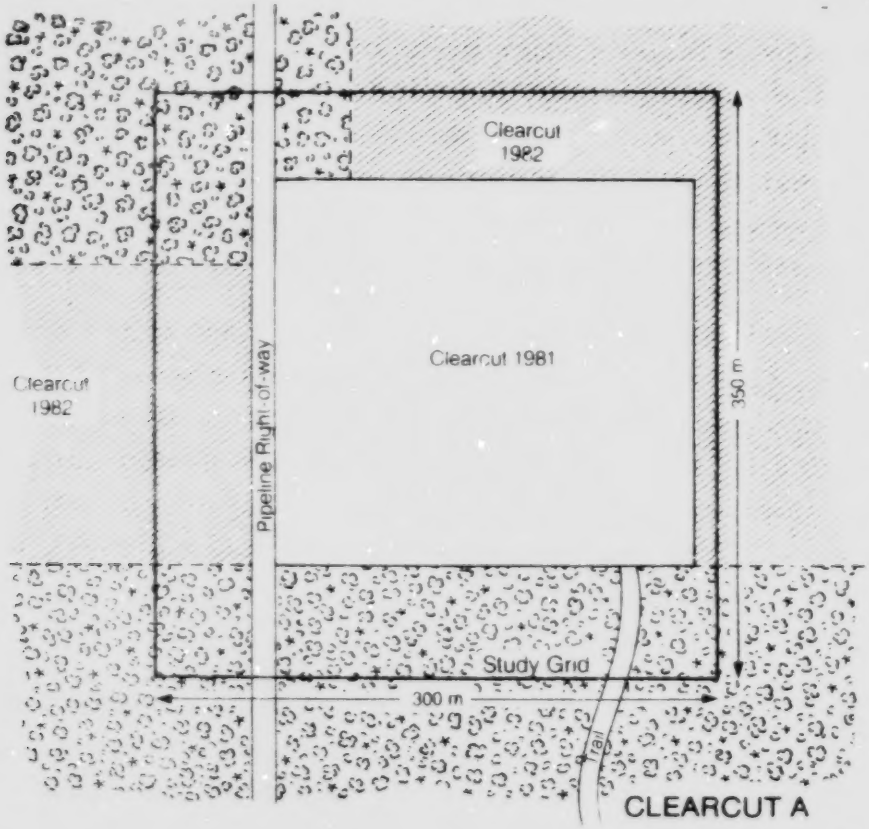


Figure 2. Orientation of study grids with respect to clearcuts in 30- and 60-year-old aspen stands.

regenerated. Grasses and other flowering plants were similarly affected by the recent land clearing. Bluejoint grass was the most abundant grass species, producing about 215 kg/ha (Appendix IV). Wild red raspberry (138.5 kg/ha) and aspen (92.1 kg/ha) were the most abundant short woody shrubs, while fireweed (91.5 kg/ha) and peavine (70.3 kg/ha) were the most dominant forb species. Deadfall was only abundant on the more recently clearcut areas as trees were wind-rowed and later burned in summer 1982. There were two pools of water on the clearcut; one had dried up by June and the other remained until late summer. The study grid was relatively flat and gently sloped to the north.

3.1.2 Clearcut B Grid

Clearcut B Grid was selected to represent a clearcut in a 30-year-old aspen stand and was established in May 1982. Clearing on this study grid was also done by the Canadian Forestry Service as part of an ENFOR program. The clearcut was bounded on the west by forest and an abandoned drill site and on all other sides by forest (Figure 2). All other sides of the plot extended beyond the clearcut edge into the surrounding aspen forest.

The forested portion of Clearcut B had a canopy height of 16.6 m and a canopy depth of 7.2 m. Total canopy cover (31.4%) was relatively high, with aspen and white birch dominating in the canopy. Tall shrubs offered a relatively low amount of cover (6.7%), while cover in the low shrub layer was relatively high at 36.9%. Several species were found in the low shrub layer but rose and low-bush cranberry were the most common.

The clearcut portion of the grid had no canopy cover and very little tall shrub cover (2.4%). Low shrub cover (26.0%) was more extensive than on most grids but extremely patchy. Areas near the drill site were vegetated more by grasses and less by shrubs in comparison with other parts of the clearcut. Grass cover on the clearcut portions of Clearcut B Grid was 67.0% and was totally dominated by bluejoint grass (152.0 kg/ha). Balsam poplar (171.9 kg/ha) and bracted honeysuckle (119.7 kg/ha) were the dominant short woody shrubs. Fireweed (289.3 kg/ha), peavine (28.9 kg/ha) and wild sarsaparella (35.0 kg/ha) were common forb species on this site. This grid had two pools of water in spring. The pool located on the clearcut dried up by July while a nearby pool along the forest edge

remained into late summer. A seepage area along the edge of the wellsite contained a mineral lick that received intensive use by elk in early summer. The grid was relatively flat but was gently sloping to the west.

3.1.3 Grids 14A and 14B

Grid 14A was established early in 1981 while Grid 14B was surveyed during May 1982. The two grids were located adjacent to each other in an aspen stand of fire origin. The fire, which occurred in 1968, left many small clumps of veteran trees as well as a stock of large-sized snags and deadfall.

Canopy heights and canopy depths for Grids 14A and 14B are very similar and averaged 5.7 and 2.4 m, respectively. The greater amount of canopy cover in Grid 14B (3.4%) than Grid 14A (1.7%) is simply a result of the inclusion of more veteran trees in Grid 14B. The tall shrub layer of Grids 14A and 14B provided a substantial amount of cover and was comprised mainly of green alder, aspen and willow. The amount of cover in the low shrub layer was small in both grids while ground cover was relatively abundant. Production of bluejoint grass (358.2 kg/ha) reached its highest levels in the 14-year-old grids while rose (43.3 kg/ha) and wild red raspberry (36.4 kg/ha) were common short woody shrubs. Fireweed produced the greatest amount of biomass (314.7 kg/ha) recorded for a single species across all study grids. This undoubtedly reflected the recent fire origin of the 14-year-old aspen stands. No standing water was found in Grid 14A, while Grid 14B had a few wet depressions along the north and west sides of the grid. These areas were characterized by high densities of willow. Grid 14B was generally flat but rolling and sloped to the southwest while Grid 14A was generally flat but sloped towards the southeast.

3.1.4 Grids 30A, 30B and 30C

Grid 30A was surveyed and marked early in 1981. This plot was found to be atypical of boreal aspen forests and the other study grids because of the many wet depressions found within the relatively level site. Two additional grids (30B, 30C) were located and established in the spring of 1982. The southeast corner of Plot 30C was deleted from sampling because of drilling activity.

Predictably, average canopy height (14.5, 15.4, 14.3 m) and average canopy depth (5.2, 5.2, 5.8 m) placed the 30-year-old grids (30A, 30B, 30C, respectively) between younger and shorter stands and older and taller stands. Aspen, balsam poplar and white birch (in the case of Plot 30C) were the dominant canopy species of the 30-year-old plots. The amount of cover in the tall shrub layer was similar among the 30-year-old grids with willow and green alder occurring as the dominant species. There was a considerable difference in the amounts of cover provided by low shrubs among the 30-year-old grids. These differences are likely a result of the variation in microtopographic features among the 30-year-old grids. Like the low shrub layer, grasses and other flowering plants offered a variable amount of cover. For example, grasses accounted for only 4.5% of the ground cover of Plot 30C but made up only 30.0% and 20.2% of Grids 30A and 30B, respectively. Grid 30A was characterized by bluejoint grass (249.9 kg/ha) as the dominant grass species and by rose (40.3 kg/ha) as the most common short woody shrub. Although Grid 30A had the highest forb species diversity (33 species) of the grids sampled in 1981, common yarrow (94.3 kg/ha) white meadowsweet (99.8 kg/ha), aster (129.7 kg/ha) and fireweed (215.4 kg/ha) accounted for over 60% of the total biomass produced. Slope and wetness of these plots may reflect some of the observed variability among the 30-year-old grids. Grid 30C was on a gentle, north-facing slope and was well-drained. Grid 30B was also on a gentle, north-facing slope but was not as well drained as Grid 30C. In contrast, Grid 30A was characterized by rolling terrain, resulting in numerous wet depressions and poor drainage.

3.1.5 Grids 60A and 60B

Grid 60A was established in January 1981 while Grid 60B was surveyed in May 1982. Total canopy cover provided by 60A and 60B was 32.8% and 33.6%, respectively. Aspen and balsam poplar were dominant canopy species while conifers made up one-eighth to one-sixth of the total canopy cover. The tall shrub layer was similar in both 60-year-old grids and was dominated by green alder. Similarly, there was little variation in cover provided by the low shrub layer in both grids but bracted honeysuckle was the dominant species in 60A while 60B was dominated by rose. The amount of cover provided by the ground layer was generally low. Bluejoint grass (128.1 kg/ha) was again the dominant grass species while bluefly honeysuckle (38.9 kg/ha), bracted honeysuckle (32.8 kg/ha) and wild red raspberry (33.8 kg/ha) were the dominant forbs.

Core samples of selected trees showed that the average age of Grid 60A was 60 years, however two age classes (30 and 60 years) were evident in Grid 60B. Grid 60A tended to slope gently to the northeast while Grid 60B sloped gently to the northwest. Both plots had intermittent streams in spring but these had dried up by late June.

3.1.6 Grid 80A

Grid 80A was established in an overmature aspen forest during May 1982. Trees forming the canopy of Grid 80A averaged 22.4 m and were much taller than those of any other forested grid. A canopy depth of 6.1 m was recorded. The amount of cover in the tall shrub layer was 17.1% and dominated by green alder. About three-quarters of the cover provided by the low shrub layer resulted from low-bush cranberry, bracted honeysuckle and rose. The abundance of cover in the ground layer was relatively low. No forb, grass or short woody shrub biomass estimates were available for the 80-year-old aspen stand. Snags and deadfall were more abundant in Grid 80A than in the other grids. Core samples of representative trees were found to range in age from 75 to 83 years. The terrain of Grid 80A was gently sloping to the northeast. Two permanent, small pools were located in the southwest corner of the grid.

3.2 HABITAT COMPOSITION BY FOREST AGE CLASS

Specific data concerning density, dbh and crown volume for differently aged forest stands were only collected for the 14-, 30- and 60-year-old grids in 1981. The 14-year-old grid was burned over in 1968 and is characterized by relatively high densities of young aspen (Table 2). Aspen was also dominant (1393 stems/ha) in the 30-year-old grid, while balsam poplar and white birch were co-dominants in the 60-year-old grid. White spruce was present in the 60-year-old stand at low densities (27 stems/ha) and indicates the progression of the stand to a climatic climax white spruce forest. Total tree densities increased sharply from the clearcut to the 14-year-old stage (4250 stems/ha) and then decreased to a low of 1380 stems/ha in the 60-year-old grid (Figure 3). Plates 1-3 illustrate vegetation development in the various aged stands.

Data on dbh and canopy volume of trees measured on the study grids are summarized in Table 3. The variability in the measurements was particularly wide on the 14-year-old grid, where results were influenced by the presence of a number of large veteran trees that survived the fire. These veteran trees had a bole diameter that exceeded 35 cm dbh and canopy volumes ranging from 518 to 1282 m^3. When these veteran trees are omitted from the sample, the average canopy volume of aspen on the 14-year-old grid is reduced from 20.45 m^3 to 3.19 m^3. Species such as green alder and willow had larger canopy volumes than aspen, balsam poplar or white birch on the 14-year-old grid. However, while the canopy volumes for willow and green alder generally remained the same from the 14- to 60-year-old stands, volume estimates increased markedly for aspen, balsam poplar and white birch (Table 3).

Basal area measurements of trees in the 10 study grids were obtained in 1982. Aspen stems had the largest basal area values in the 14, 30, 60 and 80 year forest age classes (Table 4). Tree-sized stems of green alder and willow were most common in the 14-year-old age class and may reflect their common occurrence in early successional stages. In contrast to density, total basal area progressively increased to the 60-year-old age class (21.87 sq m/ha) and then decreased slightly to 18.70 sq m/ha in the 80-year-old stands (Figure 3).

Shrub densities of the 15 most commonly occurring species in the Medicine Lake study area were highest in the clearcut (60,851 stems/ha) and 80-year-old (61,594 stems/ha) age classes (Table 5). Densities decreased to a low of

Table 2. Tree species densities per ha by forest age class in the Medicine Lake study area, 1981.

Tree Species	14 yrs	30 yrs	60 yrs
Aspen	2512	1393	173
Balsam poplar	336	713	340
White birch	96	60	473
White spruce	0	0	27
Green alder	384	313	240
Willow	928	487	127
TOTAL	4256	2966	1380

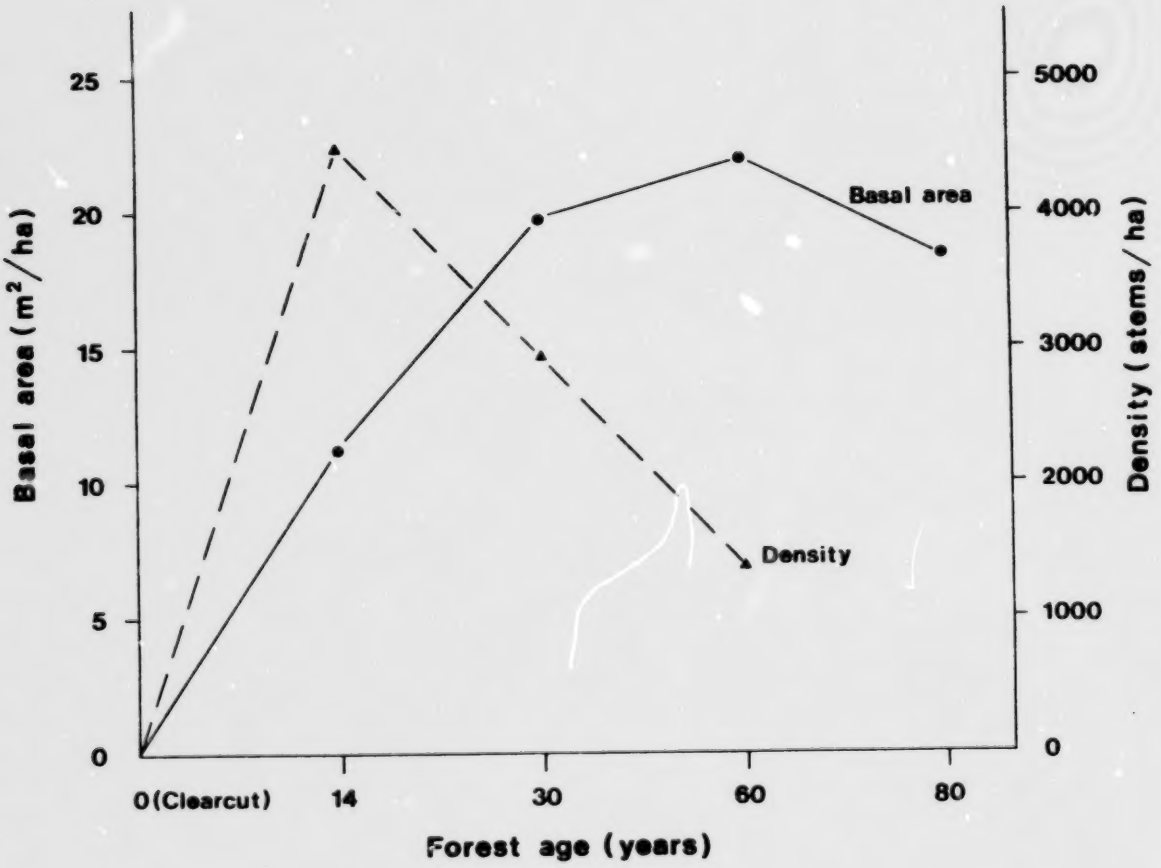


Figure 3. Relationship between forest age class and tree basal area and tree density in the Medicine Lake study area.

Plate 1. Vegetation development in boreal aspen stands at age 14 years (A), 30 years (B), 60 years (C) and 80 years (D).

Plate 2. Biomass harvesting of 37-year-old aspen stand using a Dika side cutter.

Plate 3. Vegetation development on Clearcut A after 1½ growing seasons.

Table 3. Summary of data on height (m), dbh (cm) and canopy volume (m^3) of six tree species on the Medicine Lake study plots, 1981.

Species	14 yrs			30 yrs			60 yrs		
	N	$\bar{x}$	S.E.	N	$\bar{x}$	S.E.	N	$\bar{x}$	S.E.
Aspen									
Total Height	160	5.45	0.29	188	9.30	0.25	25	19.02	0.87
dbh	160	4.19	0.37	203	7.66	0.31	25	23.70	1.66
Canopy Volume	145	20.45	10.42	93	16.67	1.77	16	71.85	23.13
Balsam poplar									
Total Height	21	5.76	1.05	104	11.01	0.30	60	16.03	0.79
dbh	21	4.70	0.89	104	10.52	0.46	60	20.26	1.36
Canopy Volume	18	19.46	13.94	70	32.27	5.24	42	62.72	11.75
White birch									
Total Height	6	4.38	0.13	9	9.31	0.94	52	9.21	0.50
dbh	6	3.28	0.30	9	9.04	1.15	68	8.32	0.62
Canopy Volume	6	4.05	0.95	8	35.17	11.09	44	39.65	11.79
White spruce									
Total Height	-			-			4	13.56	1.19
dbh	-			-			4	23.10	1.28
Canopy Volume	-			-			4	56.40	
Green Alder									
Total Height	7	4.71	0.42	11	5.09	0.35	17	5.19	0.27
dbh	24	3.51	0.20	47	4.04	0.23	36	3.99	0.23
Canopy Volume	7	24.91	10.40	10	14.56	4.39	16	20.40	4.32
Willow									
Total Height	15	5.17	0.20	18	6.39	0.47	8	7.63	0.46
dbh	56	3.50	0.08	75	5.83	0.33	19	8.94	0.80
Canopy Volume	7	45.37	10.59	17	41.57	10.59	6	45.08	12.43

Table 4. Basal area (m^2/ha) of trees by forest age class in the Medicine Lake study area.

Species	14 yrs		30 yrs		60 yrs		80 yrs	
	No.	Basal Area	No.	Basal Area	No.	Basal Area	No.	Basal Area
Aspen	150	6.52	739	11.98	499	13.32	160	10.67
Balsam poplar	33	1.43	349	5.37	287	7.61	106	7.07
White birch	6	0.24	82	1.66	52	1.30	4	0.27
White spruce	1	0.04	9	0.20	74	1.96	11	0.73
Lodgepole pine	0	0.00	15	0.33	1	0.04	0	0.00
Green alder	26	1.13	6	0.09	2	0.05	0	0.00
Willow	38	1.65	16	0.26	5	0.12	0	0.00
TOTAL	254	11.01	1216	19.94	920	21.87	281	18.7

Table 5. Shrub species densities (stems/ha) by forest age class in the Medicine Lake study area, 1982.

Shrub Species	Clearcut	14 yrs	30 yrs	60 yrs	80 yrs
Aspen	16,582	608	-	225	964
Balsam poplar	14,786	204	86	227	535
White birch	670	198	254	672	428
White spruce	-	-	17	-	-
Green alder	265	6,574	4,523	5,022	10,397
Willow	8,354	6,589	1,907	388	214
Beaked hazelnut	-	1,047	68	130	-
Low-bush cranberry	1,155	4,954	7,626	7,889	15,206
Red-osier dogwood	-	-	103	292	214
Saskatoon	330	99	86	97	964
Currant	-	50	489	1,159	857
Rose	4,269	5,489	6,000	7,632	12,759
Raspberry	5,181	1,644	2,547	6,017	7,464
Bracted honeysuckle	9,259	1,671	3,679	7,578	11,164
Other Species*	-	-	188	349	428
TOTAL	60,851	29,127	27,573	37,677	61,594

* Includes: snowberry, buffaloberry, twining honeysuckle, meadow-sweet and mountain ash.

27,573 stems/ha in the 30-year-old grids. Regenerating balsam poplar and aspen were the dominant shrub species in the clearcuts, while low-bush cranberry, rose, bracted honeysuckle and green alder dominated the shrub layer of the 80-year-old age class. Densities of green alder, low-bush cranberry and rose increased markedly as stand age increased from clearcut to 80 years (Table 5).

All the habitat variables examined for the forest age class comparisons showed highly significant differences ($P < 0.01$) (Table 6). Total canopy cover of the clearcut and 14-year-old age classes were not significantly different ($P > 0.05$) from each other but offered substantially less ($P < 0.05$) overhead cover than the remaining forest age classes. The 30-, 60- and 60-year-old edge age classes were similar to each other with respect to total canopy cover. Generally, total canopy cover increased from a low in the clearcut to a peak in the 60 year age class (Figure 4). Aspen (13.1%) and balsam poplar (11.0%) were the dominant canopy species in the 60 year plot (Table 7).

Average canopy height increased with increasing stand age and was significantly greater ($P < 0.05$) in the 80-year-old than in the remaining age classes (Table 6). Canopy depth similarly increased with age but the maximum depth was reached in the 60-year-old age class. Canopy depth decreased slightly in the 80-year-old stands.

Differences in cover provided by the tall shrub layer showed statistically more overlap among the different forest age classes (Table 6). Clearcut and 60 year edge stands provided the least cover ($P < 0.05$), while the 14-year-old age class had significantly more tall shrub cover than the remaining age classes. The tall shrub layer provided little cover in the clearcut but it increased greatly in the 14-year-old age class (Figure 4). Tall shrub cover then decreased with increased age. Green alder is the predominant tall shrub species in the 30, 60, 80 and 30 year edge age classes (Table 7). Balsam poplar and willow commonly occur in the clearcut, while the 14-year-old tall shrub layer is typified by aspen, willow and green alder.

The 80-year-old age class provided the highest ($P < 0.05$) amount of low shrub cover among all age classes (Table 6). Total low shrub cover decreased from the clearcut to a low in the 14-year-old age class but increased sharply thereafter, peaking in the 80-year-old age class (Figure 4). Low-bush cranberry, rose and

Table 6. Comparisons of selected habitat variables (% cover) by forest age class in the Medicine Lake study area.

Habitat Variable	Overall Difference	Clearcut		14 yrs		30 yrs		60 yrs		80 yrs		30 yr edge		60 yr edge	
		$\bar{x}$	S.E.	$\bar{x}$	S.E.	$\bar{x}$	S.E.	$\bar{x}$	S.E.	$\bar{x}$	S.E.	$\bar{x}$	S.E.	$\bar{x}$	S.E.
Total Canopy Cover	$P < 0.01$	0.0^{a}		2.6^{a}	0.7	31.8^{c}	1.0	33.2^{c}	1.2	19.9^{b}	1.2	13.8^{b}	1.6	31.4^{c}	3.2
Total Tall Shrub Cover	$P < 0.01$	3.1^{a}	0.9	31.9	1.9	24.5^{e}	1.0	21.7^{cde}	1.1	17.1^{b}	1.3	23.5^{de}	3.6	6.7^{a}	1.1
Total Low Shrub Cover	$P < 0.01$	19.8^{bc}	1.8	13.4^{a}	1.2	23.8^{c}	1.0	32.3^{de}	1.3	44.5^{c}	1.8	14.3^{ab}	1.6	36.9^{e}	2.6
Ground Cover	$P < 0.01$	41.6^{c}	2.4	41.0^{c}	1.8	32.7^{a}	1.1	30.7^{a}	1.2	32.3^{a}	1.8	40.7^{bc}	4.8	35.7^{ab}	3.3
Canopy Height (m)	$P < 0.01$	0.0^{a}		5.6^{b}	0.8	14.7^{c}	0.2	18.1^{d}	0.2	22.4^{e}	0.5	16.1^{cd}	0.5	16.6^{d}	0.5
Canopy Depth (m)	$P < 0.01$	0.0^{a}		2.4^{b}	0.4	5.4^{c}	0.1	7.0^{e}	0.2	6.1^{d}	0.2	7.3^{e}	0.4	7.2^{e}	0.3
No. of Plots		98		138		342		240		120		29		43	

Note: Mean values with different superscripts are significantly different ($P < 0.05$).

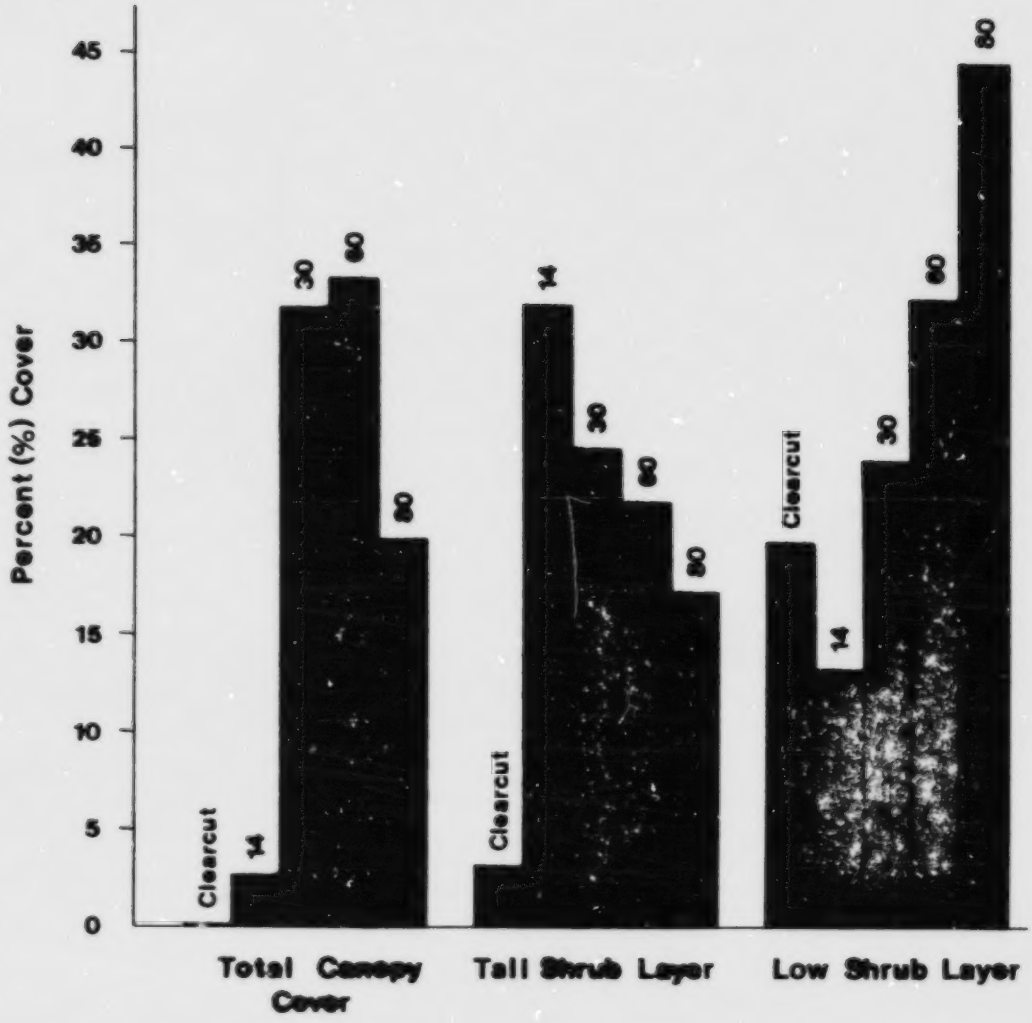


Figure 4. Comparison of canopy cover, tall shrub layer and low shrub layer between forest age stands in the Medicine Lake study area.

Table 7. Mean values of habitat variables (% cover) in relation to forest age class in the Medicine Lake study area, 1982.

Vegetation Layer	Habitat Variables	Clearcut		14 yrs		30 yrs		60 yrs		80 yrs		30 yr edge		60 yr edge	
		x̄	S.E.	x̄	S.E.	x̄	S.E.	x̄	S.E.	x̄	S.E.	x̄	S.E.	x̄	S.E.
No. of Plots		98		138		342		240		120		29		43	
CANOPY	Aspen	0.0		1.7	0.5	16.0	0.8	13.1	0.8	9.8	0.9	8.5	1.5	14.1	2.3
	Balsam poplar	0.0		0.4	0.1	10.0	0.8	11.0	0.9	8.9	1.0	3.8	1.4	5.3	1.5
	White birch	0.0		0.5	0.4	5.3	0.6	4.3	0.7	0.4	0.2	1.5	0.6	11.7	2.5
	Conifers	0.0		0.1	0.1	0.7	0.2	4.7	0.8	0.8	0.4	0.0		0.0	
	TOTAL COVER	0.0		2.6	0.7	31.8	1.0	33.2	1.2	19.9	1.2	13.8	1.6	31.4	3.2
TALL SHRUB	Aspen	0.6	0.2	7.9	0.9	0.6	0.1	0.2	0.1	0.1	0.1	0.9	0.3	0.2	0.1
	Balsam poplar	1.2	0.6	4.6	0.8	0.5	0.1	0.7	0.2	1.1	0.2	1.2	0.6	0.0	
	White birch	0.2	0.2	1.9	0.5	1.0	0.2	2.5	0.3	1.6	0.3	0.5	0.3	3.3	0.6
	Willow	1.0	0.5	7.8	1.0	8.9	0.6	2.9	0.4	0.1	0.1	4.8	1.3	1.9	0.8
	Green alder	0.2	0.1	9.9	1.3	13.4	0.8	11.7	0.8	10.9	1.1	16.5	2.7	0.8	0.3
	Conifers	0.0		0.0		0.2	0.1	3.7	0.5	3.4	0.8	0.0		0.3	0.1
	TOTAL COVER	3.1	0.9	31.9	1.9	24.5	1.0	21.7	1.1	17.1	1.3	23.5	3.6	6.7	1.1
LOW SHRUB	Aspen	8.5	1.2	0.3	0.1	0.1	0.1	0.1	0.1	0.5	0.1	1.3	0.5	2.0	0.8
	Balsam poplar	3.5	0.6	0.0		0.0		0.2	0.1	0.7	0.1	0.6	0.4	3.5	1.2
	White birch	0.4	0.2	0.1	0.1	0.2	0.1	0.6	0.1	0.3	0.1	0.0		0.8	0.2
	Willow	2.4	0.3	2.1	0.7	1.3	0.2	0.6	0.1	0.2	0.1	0.9	0.2	0.3	0.1
	Green alder	1.9	0.3	1.9	0.4	1.6	0.1	2.0	0.2	6.2	0.8	3.9	0.8	0.5	0.2
	Low-bush cranberry	0.2	0.1	2.7	0.5	6.2	0.5	5.3	0.4	10.9	0.8	2.0	0.6	7.2	1.4
	Rose	1.5	0.3	3.0	0.4	6.0	0.4	7.8	0.6	10.5	0.9	2.2	0.4	9.6	1.5
	Bracted honeysuckle	0.7	0.2	1.1	0.2	5.3	0.4	11.7	0.8	11.3	1.1	2.4	1.1	4.6	0.7
	Other Species	0.8	0.2	2.1	0.5	3.0	0.3	4.3	0.4	4.0	0.4	1.0	0.3	8.6	1.5
	TOTAL COVER	19.8	1.8	13.4	1.2	23.8	1.0	32.3	1.3	44.5	1.8	14.3	1.6	36.9	2.6
GROUND LAYER	Bare soil	7.2	1.3	0.0		0.0		0.1	0.1	0.0		4.0	1.4	0.2	0.1
	Leaf litter	0.0		8.2	0.8	17.1	0.9	11.6	0.9	2.9	0.4	3.0	1.1	3.3	0.5
	Water	1.3	0.6	0.3	0.2	0.0		0.1	0.1	0.0		1.3	1.2	0.9	0.8
	Monocots	48.3	2.7	32.7	2.0	19.0	1.3	19.1	1.4	27.3	2.0	35.0	5.1	31.6	3.5
	Dicots	32.6	2.0	50.8	1.7	50.6	1.0	45.4	1.1	38.4	1.6	47.2	4.5	40.4	3.1
	Horsetail	0.3	0.1	0.1	0.1	0.5	0.1	1.0	0.1	0.6	0.2	0.1	0.1	0.9	0.2
	Moss	0.0		0.8	0.1	1.3	0.1	2.8	0.3	0.4	0.1	1.2	0.5	0.5	0.2
CANOPY HEIGHT (m)		0.0		5.6	0.8	14.7	0.2	18.1	0.2	22.4	0.5	16.1	0.5	16.6	0.5
CANOPY DEPTH (m)		0.0		2.4	0.4	5.4	0.1	7.0	0.2	6.1	0.2	7.3	0.4	7.2	0.3

bracted honeysuckle were the dominant species in the 80-year-old stands (Table 7).

Ground cover was significantly higher in the clearcut and 14-year-old age classes than the 30-, 60- and 80-year-old age classes (Table 6). Monocots (grasses) dominated the youngest age class and decreased as stand ages increased (Table 7). Moss cover was highest on the 14 and 30 year age classes and lowest in the clearcuts. The occurrence of mosses was greatest in the 60-year-old age class and was likely associated with the minor white spruce component found there.

There were significant differences ($P < 0.05$) in forb production among the five age classes sampled (Table 8). Greater ($P < 0.05$) amounts of forbs were produced in the 14 and 30 year age classes. Grass production was highest in the 14-year-old grid. Significantly greater ($P < 0.05$) amounts of short woody plants were produced in the two clearcut grids than in the older stands. Fireweed and bluejoint grass dominated the ground cover species in the 14-year-old age class, while the 30-year-old age class was characterized by high production of fireweed, aster and bluejoint grass (Appendix III and IV).

Table 8. Comparisons of forb, grass and short woody shrub production (kg/ha) by forest age class in the Medicine Lake study area, 1981.

	Overall Difference	Clearcut A		Clearcut B		14 yrs		30 yrs		60 yrs	
		$\bar{x}$	± S.E.	$\bar{x}$	± S.E.	$\bar{x}$	± S.E.	$\bar{x}$	± S.E.	$\bar{x}$	± S.E.
Forbs	P< 0.05	537.1^{a}	75.8	541.7^{a}	92.1	697.7^{b}	89.9	889.6^{b}	118.1	521.7^{a}	82.4
Grasses	P< 0.01	235.3^{b}	58.0	152.5^{a}	26.0	400.6^{c}	72.7	262.9^{b}	72.2	130.4^{a}	35.5
Short Woody Shrubs	P< 0.01	469.9^{a}	103.8	490.4^{a}	93.6	132.1^{b}	26.3	126.4^{b}	29.5	165.5^{b}	33.1
TOTAL		1242.3		1184.6		1230.4		1278.9		817.6	
No. of Plots		23		25		25		25		24	

Note: Mean values with different superscripts are significantly different (P< 0.05).

3.3 BREEDING BIRD USE OF THE STUDY GRIDS

This section briefly describes the avifauna associated with each of the study grids. Use of the various successional stages and special habitats (eg. ecotones, ponds, snags and deadfall) by the 60 bird species recorded in the study area is summarized in Appendix VII. A list of common and scientific names of birds and codes referred to in the report are given in Appendix VIII.

3.3.1 Clearcut Grids

Bird use of clearcut areas in 1981 was limited. Three shorebird species (killdeer, common snipe, solitary sandpiper) and one finch (Lincoln's sparrow) set up territories on Clearcut A. Their presence can be at least partially attributed to habitat created by clearcutting and to scattered wet depressions.

In 1982, the clearcuts were one year old and sucker growth from the summer of 1981 was well established. Shorebird species were present on Clearcut A but they did not appear to occupy territories. Lincoln's sparrows returned in higher numbers and were joined by other finches (LeConte's sparrow, chipping sparrow, clay-colored sparrow, white-throated sparrow) in 1982. Mourning warblers had set up territories in the dense sucker growth of Clearcut A.

Birds recorded on the edge of the forest surrounding the clearcuts represent species which occupy territories only in forest or territories which include clearcut and forest. In 1981, 16 species were recorded along the forest edge, however only six of these were found to be using the clearcut area (Appendix VII). Users of the clearcut were either feeding in the air (least flycatcher) or ground feeders (house wren, American robin, dark-eyed junco, chipping sparrow, white-throated sparrow). In 1982, there were again 16 species recorded in the forest edge. The same six species using clearcut and forest areas in 1981 were also observed using the same area in 1982. However, it appeared that an alder flycatcher had also established a territory along the forest edge.

Sparrows were the dominant birds of the clearcut habitat. Chipping sparrows, clay-colored sparrows, white-throated sparrows and Lincoln's sparrows on Clearcut A and LeConte's sparrows on Clearcut B were recorded in more grid blocks than any other species. Both species diversity and the total number of breeding bird territories were lowest on the clearcut grids (Table 9).

Table 9. Average density (1981, 1982) of breeding bird territories (per 100 ha) recorded by forest age class on the Medicine Lake study area.

Bird Species	Clearcut	14 yrs	30 yrs	60 yrs	80 yrs
Goshawk				P*	
Broad-winged hawk			P		
Marsh hawk	P				
Ruffed grouse		P	P		
Killdeer	6.0				
Common snipe	6.0	P	P		
Spotted sandpiper	P				
Solitary sandpiper	6.0				
Mourning dove		P			
Ruby-throated hummingbird	P			P	
Common flicker		5.7			P
Pileated woodpecker				P	
Yellow-bellied sapsucker		P		P	8.4
Hairy woodpecker	P				
Alder flycatcher	3.0	17.2	5.4		P
Least flycatcher		177.7	2.2	19.7	P
Tree swallow		P			
Black-capped chickadee		11.5	6.5	12.6	8.4
Boreal chickadee					P
Red-breasted nuthatch		8.6	4.4	5.6	8.4
House wren		5.7			
American robin		5.7	1.1	P	P
Hermit thrush		2.9	4.4		
Swainson's thrush		5.7	13.1	23.9	8.4
Mountain bluebird		P			
Golden-crowned kinglet				2.8	
Ruby-crowned kinglet				P	P
Cedar waxwing		P			
Solitary vireo			P		P
Red-eyed vireo		43.0	33.7	29.5	12.6
Warbling vireo		25.8	6.5	7.0	8.4
Black and white warbler		28.7	14.2	14.0	
Tennessee warbler		28.7	31.6	44.9	16.8
Orange-crowned warbler		8.6	P	1.4	
Yellow warbler		57.3			
Yellow-rumped warbler		5.7	6.5	8.4	12.6
Black-throated green warbler			P	5.6	4.2
Ovenbird			66.4	36.5	8.4
Connecticut warbler			4.4	P	P
Mourning warbler	11.9	17.2	22.9	29.5	33.7
American redstart		45.9	10.9	16.8	
Red-winged blackbird		P			
Northern oriole		5.7	P		P
Rusty blackbird		P			P
Brown-headed cowbird		5.7		P	
Western tanager				2.8	
Rose-breasted grosbeak		22.9	8.7	5.6	8.4
Evening grosbeak				2.8	
American goldfinch	P				
LeConte's sparrow	11.9				
Dark-eyed junco		17.2	10.9	11.2	P
Chipping sparrow	6.0	8.6	22.9	39.3	42.1
Clay-colored sparrow	26.8	17.2	1.1		P
White-throated sparrow	6.0	77.4	32.7	60.4	50.5
Lincoln's sparrow	26.8		2.2		P
No. of Bird Species	10	25	22	21	14
Total Territories per 100 ha	110.2	656.2	312.4	380.3	231.3
Species Diversity**	0.89	1.15	1.14	1.16	1.02

*P indicates the presence of a species whose territory was not mappable.

**Species diversity = $-\Sigma P_i \log P_i$

3.3.2 Grids 14A and 14B

Sixteen species of birds occupied territories on Grid 14A in 1981 (Appendix VI). None of these species held territories on Clearcut A. The list of territorial bird species on Grid 14A included a flycatcher, chickadee, nuthatch, thrush, two vireos, five warblers, an oriole and four finch species. The least flycatcher had the highest density of territories.

In 1982, 22 territorial bird species were recorded on the 14-year-old plots. The additional territorial species observed included a woodpecker, a second flycatcher, a wren, another thrush, two warblers, a blackbird and one finch. The least flycatcher was again the most abundant species. In comparison with the clearcut grids in 1982, the birds of the 14-year-old grids showed a shift from ground-feeding finches to insect-feeding birds of a number of families.

The majority of the grid blocks of Grid 14A appeared to be suitable as least flycatcher habitat. No other species was found so extensively in this plot. In Grid 14B, the least flycatcher occurred in more grid blocks than any other species, however the alder flycatcher, black and white warbler, yellow warbler and white-throated sparrow were also relatively common. The total number of breeding bird territories in 14-year-old grids was higher than that of all other grids (Table 9). Because red-eyed vireos, Tennessee warblers and northern orioles were generally associated with veteran trees on the 14-year-old grids, the density of bird territories representative of a 14-year-old aspen stand may be somewhat inflated. Snags found throughout these grids provide feeding and singing perches for least flycatchers. The snags and their effect on the density of least flycatchers was likely responsible for the higher number of breeding bird territories in the 14-year-old aspen stands. Bird species diversity was similar to that found in the 30- and 60-year-old grids.

3.3.3 Grids 30A, 30B and 30C

Territories for 18 species were recorded on Grid 30A in 1981. There were no differences between the 14-year-old grid and the 30-year-old grid in the representation of bird families. Instead, there were species trades (i.e. one species was replaced by another species of the same family) or there were changes in the prominence of some species. Flycatchers declined in numbers

while numbers of thrushes, vireos and Tennessee warblers increased. Ovenbirds and Connecticut warblers appeared at the 30-year stage while yellow warblers disappeared.

In 1982, the territories of 19 species were mapped for the three 30-year-old grids. There were three fewer species than on the 14-year-old plots in the same year. Rarer species such as the orange-crowned warbler, northern oriole and clay-colored sparrow did not have mappable territories in the 30-year-old grids but were present in the 14-year-old plots.

The ovenbird became the dominant bird by the 30-year-old stage as indicated by its occurrence in more grid blocks than any other species, however the occurrences of red-eyed vireos and Tennessee warblers were almost as widespread. The density of breeding bird territories dropped from that found in the 14-year-old stands while species diversity was marginally lower (Table 9).

3.3.4 Grids 60A and 60B

Sixteen species were recorded on territories on Grid 60A in 1981 (Appendix VI). There were few differences in species composition when compared to Grid 30A in 1981. Most observed differences are likely a result of small sample sizes. Alder flycatchers, least flycatchers, red-breasted nuthatches, hermit thrushes, Connecticut warblers, clay-colored sparrows and Lincoln's sparrows were found on Grid 30A but not on Grid 60A. Golden-crowned kinglets, warbling vireos, yellow-rumped warblers, black-throated green warblers and dark-eyed juncos were not recorded on Grid 30 but were relatively common on Grid 60A. Presumably the appearance of the golden-crowned kinglet and black-throated green warbler territories is associated with the increase in conifers on the 60-year-old plots.

In 1982, 19 species were observed on territories in the 60-year-old grids. A similar number of species were found on the 30-year-old grids during the same year. Differences in the species composition of the 30- and 60-year-old grids were again largely a result of sample size. The alder flycatcher, red-breasted nuthatch, American robin, hermit thrush and Connecticut warbler occupied territories on 30-year-old grids but not on the 60-year-old grids. Conversely, the least flycatcher, orange-crowned warbler, black-throated green warbler and

western tanager occupied territories on 60-year-old grids but not on the 30-year-old grids. Only the black-throated green warbler and western tanager territories appear related to the presence of more mature forests.

The ovenbird remained the dominant species in 60-year-old forests. Chipping sparrows were equally widespread, having increased in numbers with respect to the 30-year-old forest stage. Red-eyed vireos maintained a similar level of dominance to that found in the 30-year-old grids and did not surpass the numbers of ovenbirds or chipping sparrows in the 60-year-old grids. The density of breeding bird territories, like that of the 30-year-old grids, was less than that of the 14-year-old stand but it was higher than that of the 80-year-old stand (Table 9). Species diversity was similar to that found in the 14- and 30-year-old grids.

3.3.5 Grid 80A

Sixteen species of birds occupied territories on Grid 80A in 1982. The 30-year-old and 60-year-old grids had only three more species in 1982. Black and white warblers and American redstarts were absent on Grid 80A, possibly reflecting the low amount of cover available in the canopy and tall shrub layers. Only three woodpecker territories were defined in all of the breeding bird grids and two of these were mapped on Grid 80A. The nests of a hairy woodpecker and a yellow-bellied sapsucker were found in diseased aspen trees. A hairy woodpecker nest was also found near, but not in, Grid 60B.

Mourning warblers, chipping sparrows and white-throated sparrows were the dominant species of Grid 80A. The presence of these species reflect the concentration of cover for birds in the low shrub and ground layers. It is interesting to note that the mourning warbler and several species of sparrows were the dominant species on Clearcut A in 1982. The highest level of woodpecker activity was found in the 80-year-old grid. Only the clearcut grids had lower densities of breeding birds and lower indices of species diversity than Grid 80A (Table 9). While nesting and foraging aspects of these "overmature" forests makes them increasingly attractive to woodpeckers, declining canopy cover makes them less attractive to many breeding bird species.

3.3.6 Winter Bird Use

Both species diversity and density of winter bird populations were low on all of the age classes surveyed during the winter of 1980–81. Only 13 bird species were recorded as winter residents of aspen forests, in comparison to 55 bird species that occurred on the study grids during the breeding season. The greatest number of species (11) were observed in the 60-year-old stand. The highest density (125 birds/100 ha) was recorded in the 30-year-old stand (Table 10). Most abundant species were the common redpoll and black-capped chickadee, which together accounted for approximately 75% of the total. Densities of woodpeckers were highest on the 14-year-old grid and lowest on the 30-year-old grid, perhaps reflecting the observed differences in availability of snags.

Table 10. Densities of winter bird populations (per 100 ha) in 1980-81 on study grids 14A, 30A and 60A.

Species	Stand Age		
	14 yrs	30 yrs	60 yrs
Hairy woodpecker	10.0	0.8	2.5
Downy woodpecker	-	0.8	1.7
Pileated woodpecker	2.0	-	-
Blue jay	-	0.8	-
Gray jay	4.0	3.3	2.5
Black-billed magpie	6.0	2.5	2.5
Common raven	8.0	8.3	3.3
Black-capped chickadee	8.0	39.2	34.2
Boreal chickadee	-	-	1.7
White-breasted nuthatch	-	-	0.8
Common redpoll	10.0	66.7	49.2
Ruffed grouse	8.0	2.5	0.8
Goshawk	2.0	-	0.8
TOTAL	58.0	124.9	100.0

3.4 BIRD SPECIES USE IN RELATION TO FOREST AGE CLASS

3.4.1 Bird Species - Habitat Relationships

The influence of various habitat variables on the distribution of bird species was investigated using principal components analysis. This analysis reduced the 10 originally measured habitat variables to three composite habitat factors. The first three principal components extracted from the correlation matrix accounted for 83.2% of the total variance (Table 11). Only those principal components with eigen values greater than 1.0 were considered significant. By rotating the three principal components in the original 10 habitat variable space with the varimax procedure, interpretability of the principal components was significantly improved. The first principal component accounted for 57.1% of the total variation and was highly correlated with canopy height, total vegetation cover, canopy depth, deciduous canopy cover and the volume index (Table 11). Therefore, this component may be considered as being related to canopy cover. Bird species occurring in areas of high canopy cover would be expected to have high loadings on the first principal component.

An additional 15.1% of the total variance was extracted from the data set by the second principal component (Table 11). Correlations between the component and the original variables indicate a strong inverse relationship among three habitat variables. The high positive loadings on the coniferous canopy and tall shrub variables and the high negative loading on the percentage of ground cover represents a conifer related gradient. Bird species typically associated with coniferous growth would be expected to have high values for this component, since coniferous cover is generally associated with mature aspen stands in the Medicine Lake study area. Bird species which occur in areas of high grass and forb cover would have lower component scores, reflecting younger aged aspen stands.

The third principal component accounted for an additional 11.0% of the remaining unexplained variance in the data set (Table 11). A strong bipolar relationship existed between the deciduous tall and low shrub cover variables, indicating that this component reflects bird species preferences for shrub cover relative to stand age. Bird species utilizing a well developed deciduous tall shrub layer in 14- and 30-year-old aspen stands would typically have low component

Table 11. Results of a principal component analysis based on 10 habitat variables for 31 bird species in the Medicine Lake study area, 1982.

Principal Component	1	2	3
Variation Explained (%)	57.1	15.1	11.0
Cumulative Variation (%)	57.1	72.2	83.2
Variable	**Correlations with Original Variables**		
Canopy height	0.86	0.26	0.21
Total vegetation cover	0.86	0.07	-0.11
Canopy depth	0.85	0.31	0.06
Deciduous canopy cover	0.84	0.38	0.03
Volume index	0.79	0.49	0.02
Conifer canopy cover	0.24	0.92	-0.01
Conifer tall shrub cover	0.24	0.85	-0.13
Ground cover	-0.58	-0.64	-0.13
Deciduous tall shrub cover	0.25	-0.15	-0.87
Low shrub cover	0.44	0.04	0.79

scores. In contrast, bird species associated with a dense low shrub layer would have low scores for this principal component and would typically occur in recently clearcut areas and/or mature or overmature aspen forests.

By using each of the first three principal components as coordinates, a three-dimensional ordination depicting the relative positions of the 31 bird species and six differently aged aspen stands can be obtained (Figure 5). The horizontal axis, representing the first principal component show the bird species distributed along a gradient related to canopy cover. Chipping sparrows, Connecticut warblers, ovenbirds and black-capped chickadees were associated with higher amounts of deciduous canopy cover typical of the 60- and 80-year-old stands. In contrast, yellow warblers, northern orioles, LeConte's sparrows, Lincoln's sparrows and clay-colored sparrows were generally found in clearcut areas having low canopy cover.

The axis extending to the foreground represents the second principal component. This component is indicative of the presence of coniferous vegetation in the background of Figure 5 while high ground cover values are represented in the foreground. Black and white warblers tended to occur in areas with abundant grass cover. On the opposite end of this axis, black-capped chickadees and rose-breasted grosbeaks were associated with abundant conifer cover. Although the forest edges surrounding clearcuts had large amounts of conifer cover, this was not representative of the forests generally and resulted from a small sample of forest edge habitats.

The third principal component which extends along a vertical axis, shows the distribution of bird species along a gradient related to both tall and low shrub cover. It extends upward for bird species not requiring deciduous tall shrub cover to those that are dependent on cover provided by deciduous tall shrubs (Figure 5). A low shrub gradient is also associated with this component but in an opposite direction to the tall shrub gradient. The American robin, warbling vireo, yellow warbler, yellow-rumped warbler, American redstart, northern oriole and LeConte's sparrow were associated with abundant cover in the tall shrub layer. Clearcuts and 60- and 80-year-old stands were typified by an abundance of cover in the low shrub layer. Black and white warblers and brown-headed cowbirds occurred in areas having an abundance of low shrubs.

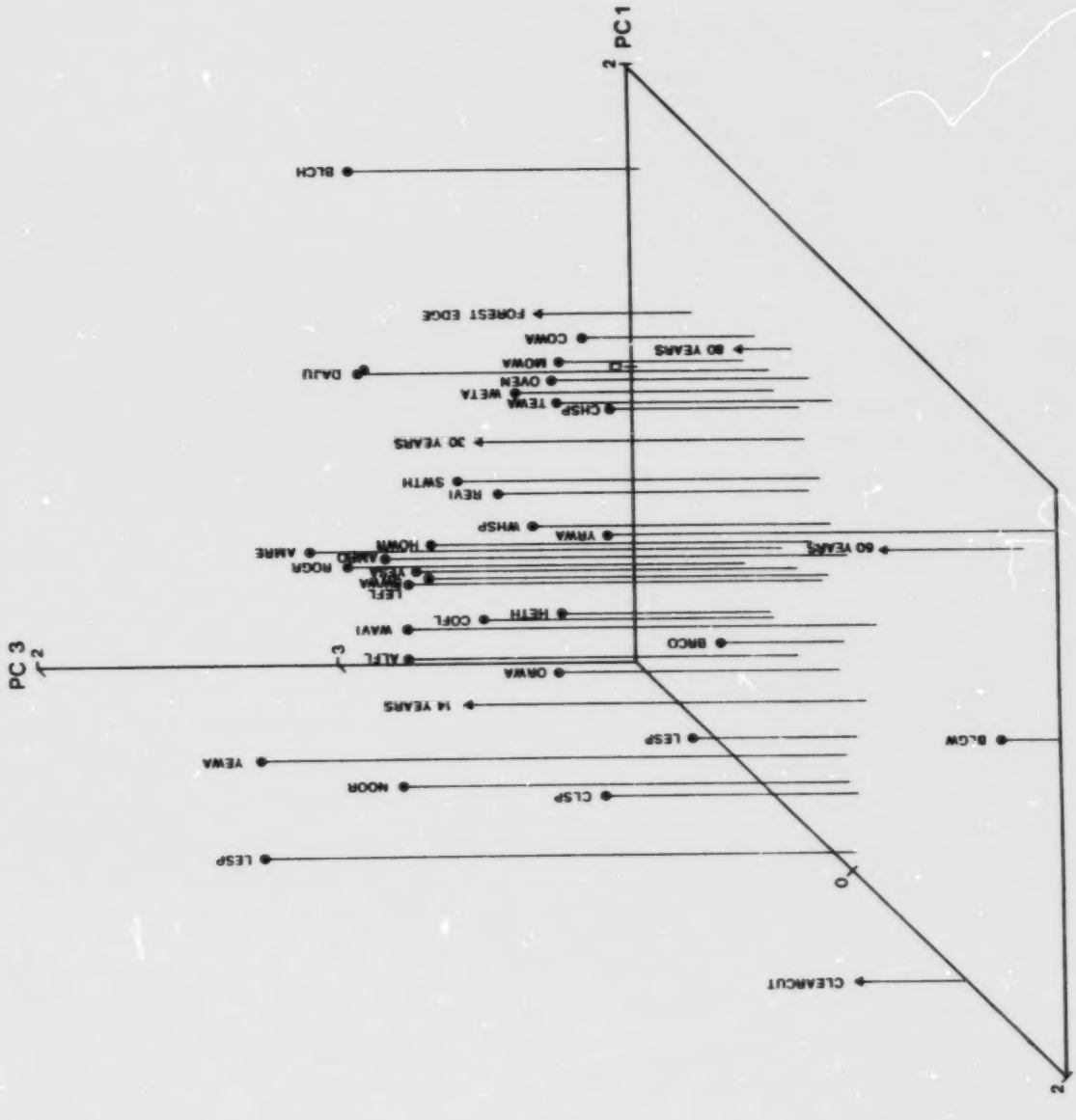


Figure 5. Three-dimensional ordination of the distribution of 31 bird species and six aspen stands of different ages in the Medicine Lake study area, 1982.

Fifteen of the 31 species included in the principal components analysis either did not show well-defined habitat preferences or occupied habitat positions that did not represent extremes for any of the principal components. These species included the common flicker, yellow-bellied sapsucker, alder flycatcher, least flycatcher, house wren, hermit thrush, Swainson's thrush, red-eyed vireo, Tennessee warbler, orange-crowned warbler, black-throated green warbler, mourning warbler, western tanager, dark-eyed junco and white-throated sparrow. Many of these species were primarily associated with 14-year-old and 30-year-old stands which similarly occupy intermediate positions with respect to amounts of deciduous canopy cover, low shrub cover, tall shrub cover, grass cover or conifer cover.

The sixteen species of birds which showed an affinity for either high or low cover values for particular habitat variables can be divided into eight groups: (1) species associated with abundant, deciduous canopy cover - the ovenbird, Connecticut warbler and chipping sparrow, (2) species associated with abundant deciduous canopy cover and with an abundance of conifer cover (or little grass cover) - the black-capped chickadee, (3) species associated with the lack of a deciduous canopy - the clay-colored sparrow and the Lincoln's sparrow, (4) species associated with the lack of a deciduous canopy and with an abundance of cover in the tall shrub layer (or the absence of low shrubs) - the yellow warbler, northern oriole and LeConte's sparrow, (5) species associated with an abundance of grass cover (or the absence of conifers) and with a dense, low shrub layer (or the absence of tall shrubs) - the black and white warbler, (6) species associated with an abundance of conifer cover (the absence of grass cover) - the rose-breasted grosbeak, (7) species associated with dense tall shrub layers (or the absence of low shrubs) - the American robin, warbling vireo, yellow-rumped warbler and American redstart and (8) species associated with a dense low shrub layer (or the absence of tall shrubs) - the brown-headed cowbird.

Sixty- and 80-year-old stands, those stands which would be reduced if aspen forests were harvested on a 30 year rotation, were characterized by high cover values for low shrubs, grass, and the deciduous canopy. Grass cover and low shrub cover values were also high in the clearcuts. Thus species closely tied to an abundance of deciduous canopy cover such as the ovenbird, Connecticut warbler, black-capped chickadee and chipping sparrow would be most adversely affected by a 30-year rotation.

3.4.2 Bird Species Associations

A 3 x 31 data matrix (3 principal components x 31 bird species) was subjected to cluster analysis. The analysis revealed that the original 31 bird species could be grouped into four different bird associations (Figure 6). These bird associations reflect groupings of individual species which exhibit similar affiliations with respect to the three major habitat variables identified during the principal components analysis. The following sections describe each bird association with respect to species composition and related habitat variables.

Bird Association 1

Bird Species

Black-capped chickadee
Swainson's thrush
Red-eyed vireo
Tennessee warbler
Ovenbird
Connecticut warbler
Mourning warbler
Western tanager
Dark-eyed junco
Chipping sparrow
White-throated sparrow

Related Habitat Variables

- high amounts of deciduous canopy cover
- moderate to high amounts of conifer cover
- low grass cover

This group of birds occurred most frequently in the 30- to 80-year-old stands. The composition of this association can be related to the characteristics of older forests - thinning canopy and the increasing abundance of snags, conifers and low shrubs. The presence of hard snags provides suitable nesting sites for black-capped chickadees while Connecticut and mourning warblers tend to inhabit areas of dense shrub growth. Swainson's thrushes, tanagers and chipping sparrows nest in conifers while a well-developed layer of leaf litter is an important feature in ovenbird habitat. The abundance of deadfall offers many nesting sites for juncos. Red-eyed vireos find a deep canopy in which to nest and to forage.

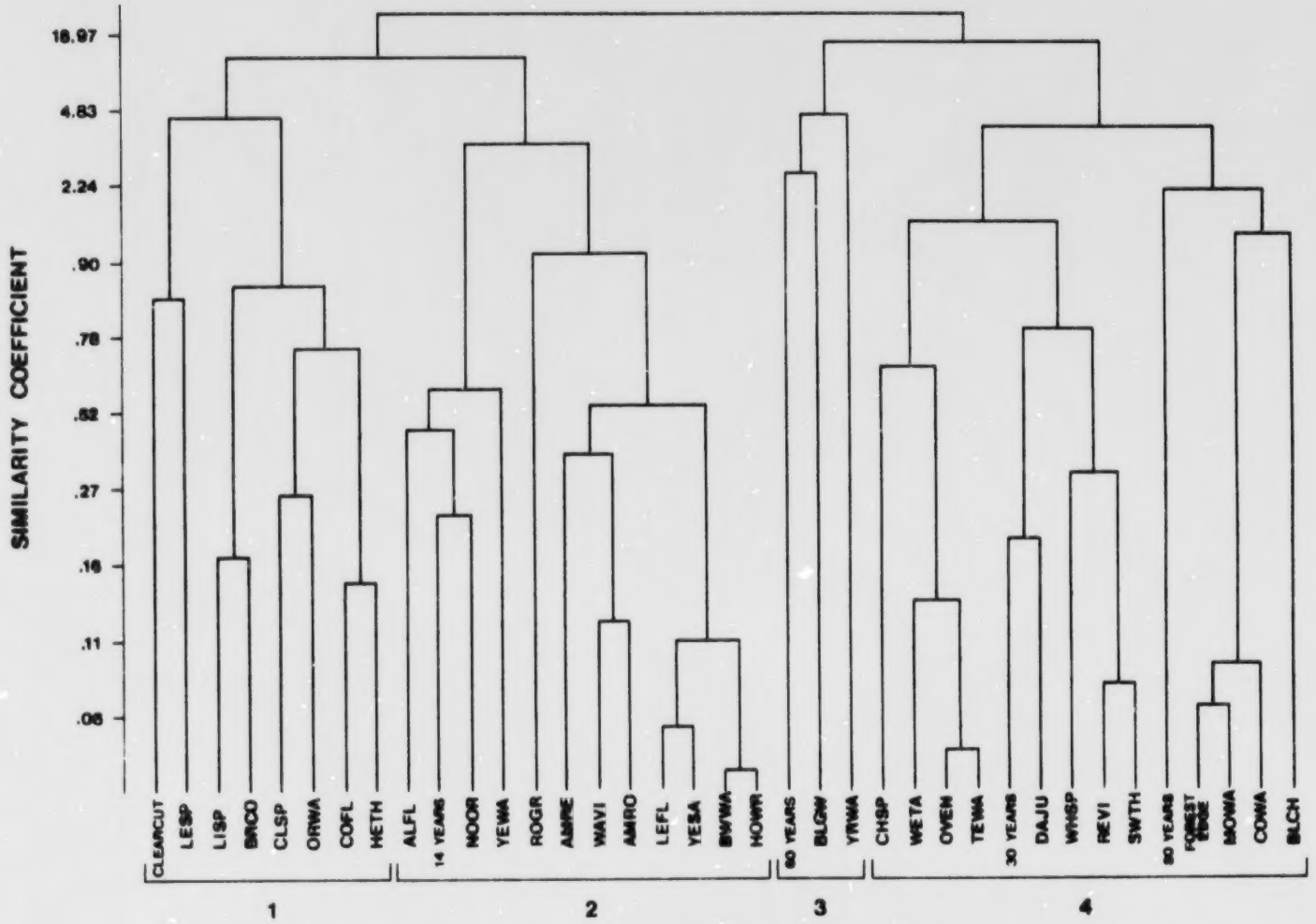


Figure 6. Dendogram illustrating habitat associations of 31 bird species in the Medicine Lake study area, 1982.

Bird Association 2

Bird Species

Yellow-bellied sapsucker
Alder flycatcher
Least flycatcher
House wren
American robin
Warbling vireo
Black and white warbler
Yellow warbler
American redstart
Northern oriole
Rose-breasted grosbeak

Related Habitat Variables

- high amount of cover in the tall shrub layer

Birds occur in this association either because they inhabit the tall shrub layer or because they are associated with some habitat feature commonly found in the 14-year-old stands which were sampled. The flycatchers, warbling vireo, warblers and rose-breasted grosbeak are typically associated with the tall shrub layer. These birds may also have benefitted from the presence of snags and veteran trees present in the 14-year-old stands. The orioles were present only in areas supporting veteran trees. Although robins nest in the tall shrub layer, they generally forage in grassy clearings where regeneration is poor. House wrens also used the grassy clearings and probably nested in the tangles of deadfall or in snags. Sapsuckers fed in the tall shrubs but must have nested off the study grids or in the veteran trees. The inclusion of some wet depressions in the study grids provided suitable habitat for alder flycatchers.

Bird Association 3

Bird Species

Common flicker
Hermit thrush
Orange-crowned warbler
Brown-headed cowbird
LeConte's sparrow
Clay-colored sparrow
Lincoln's sparrow

Related Habitat Variables

- low amounts of deciduous canopy cover
- few conifers in the canopy layer and in the tall shrub layer
- well-developed low shrub cover.

Birds in this association generally occur in open habitats supporting good low shrub growth or areas lacking mature canopy cover. Although the clearcut habitat was the only age class to cluster out in this bird association, many of the bird species were recorded in open areas of the 14-year-old aspen stands which had similar habitat features to those of the clearcut habitats. Therefore, even though birds were recorded in the clearcut and 14-year-old aspen stands, this bird association reflects bird species that prefer open habitats. For example, LeConte's sparrow occurred only in the grassy, poorly regenerating areas of the clearcuts, however the clay-colored and Lincoln's sparrows not only occurred in the suckering growths of the clearcuts but also in the poorly-regenerated grassy areas of the 14-year-old stands. The remaining birds of this cluster were recorded in the open, grassy, poorly regenerated areas of the 14-year-old stand. The attraction of the hermit thrush to such habitat is difficult to explain because this species is more typical of more mature forests or mixedwood or conifer forests. Cowbirds perched in snags over these open areas presumably searching for warbler nests in which to lay their eggs. (The yellow warbler is often parasitized by cowbirds.) Flickers foraged on the ground in these open areas, perhaps attracted by the carpenter ants in the abundant deadfall and snags. The orange-crowned warbler appeared to prefer an open, tall shrub layer.

Bird Association 4

Bird Species

Yellow-rumped warbler
Black-throated green warbler

Related Habitat Variables

- high amount of conifer and deciduous canopy cover
- high amount of conifer cover in the tall shrub layer
- high canopy volume index
- low amount of cover on the ground layer.

The two warblers of this association are typically found in conifer and mixed-wood forests. Although large conifers occurred in both the 60- and 80-year-old stands, the cluster analysis placed only the 60-year-old stand in this association because of higher conifer densities. The few observations of boreal chickadees and ruby-crowned kinglets were collected in the same areas as those of the yellow-rumped and black-throated green warblers. These chickadee and kinglet species are usually associated with conifer habitats. Such habitat would probably disappear from areas managed for harvest at 30 years of age.

3.5 BROWSE PRODUCTION AND UTILIZATION BY FOREST AGE CLASS

3.5.1 Browse Preferences of Ungulates and Snowshoe Hares

Of the 24,600 twigs tallied during browse surveys conducted in 1981 and 1982, only 4.2% (1024) had been browsed by ungulates. However, ungulates were not proportionately utilizing ($\chi^2 = 1910.3$, $P < 0.001$) the browse species available to them (Table 12). Ungulates showed preferences for willow, beaked hazelnut, low-bush cranberry and red-osier dogwood. Balsam poplar, white birch and saskatoon were browsed in proportion to their availabilities, while the remaining species were avoided. No evidence of browsing by ungulates was recorded for white spruce or currant. Since less than one-half of the species sampled in the browse surveys showed any significant utilization by ungulates, only those species that were preferred or utilized in proportion to availability are considered as principal ungulate browse species.

About 4.5% (1071) of the 23,787 twigs considered to be available to snowshoe hare were browsed. Selection for certain browse species by snowshoe hares was highly significant ($\chi^2 = 1442$, $P < 0.001$). Snowshoe hares preferred white birch, rose and raspberry over the other browse species (Table 13). Balsam poplar, aspen, white spruce, green alder, willow and bracted honeysuckle were avoided while the remaining species were browsed in proportion to their availabilities. All the species sampled during the browse surveys showed at least some sign of being browsed by snowshoe hare, however only those browse species preferred or proportionately utilized by snowshoe hare will be considered as principal browse species.

3.5.2 Browse Production

3.5.2.1 Ungulates

There were large differences in stem density of principal ungulate browse species among the different forest age classes (Table 14). Stem density of ungulate browse species was highest in the clearcut areas (27,091 stems/ha) and lowest in the 60-year-old age class (9693 stems/ha). Totals of all shrub species followed a similar trend, however the 30-year-old age class had the lowest density (27,573 stems/ha). Regenerating aspen accounted for approximately 61%

Table 12. Utilization of browse species by ungulates on the Medicine Lake study grids. Data are combined for 1981 and 1982.

Browse Species	No. of Available Twigs	Proportion of Browse		95% Confidence Interval Bonferroni Z*	Pref.**
		Expected (P_{io})	Observed (P_i)		
(Z = 2.49)					
Aspen	2,028	0.082	0.020	$0.044 \leq P_i \leq 0.090$	0
Balsam poplar	1,104	0.045	0.067	$0.007 \leq P_i \leq 0.013$	-
White birch	505	0.021	0.035	$0.018 \leq P_i \leq 0.052$	0
White spruce	457	0.019	0.000		-
Green alder	8,867	0.360	0.049	$0.029 \leq P_i \leq 0.069$	-
Willow	3,324	0.135	0.279	$0.238 \leq P_i \leq 0.320$	+
Beaked hazelnut	109	0.004	0.028	$0.013 \leq P_i \leq 0.043$	+
Low-bush cranberry	3,051	0.124	0.453	$0.408 \leq P_i \leq 0.498$	+
Red-osier dogwood	56	0.002	0.021	$0.008 \leq P_i \leq 0.034$	+
Saskatoon	32	0.001	0.003	$0.000 \leq P_i \leq 0.008$	0
Currant	302	0.012	0.000		-
Rose	2,028	0.082	0.015	$0.004 \leq P_i \leq 0.026$	-
Raspberry	361	0.015	0.002	$0.000 \leq P_i \leq 0.006$	-
Bracted honeysuckle	2,110	0.086	0.026	$0.012 \leq P_i \leq 0.040$	-
Other species***	266	0.011	0.002	$0.000 \leq P_i \leq 0.006$	-
TOTAL	24,600	0.999	1.000		

* Bonferroni statistic indicates preference or avoidance. If the proportion falls outside of the confidence interval, a significant deviation from the expected is indicated (P_i <0.05).

** Indicates whether a species was preferred (+), avoided (-), or used in proportion to its availablity (0).

*** Includes: snowberry, meadowsweet, twinning honeysuckle and mountain ash.

Table 13. Utilization of browse species by snowshoe hares on the Medicine Lake study grids. Data are combined for 1981 and 1982.

Browse Species	No. of Available Twigs	Proportion of Browse		95% Confidence Interval Bonferroni Z*	Pref.**
		Expected (P_{io})	Observed (P_i)		
(Z = 2.94)					
Aspen	1,970	0.083	0.026	$0.012 \leq P_i \leq 0.040$	-
Balsam poplar	1,083	0.046	0.010	$0.001 \leq P_i \leq 0.019$	-
White birch	502	0.021	0.050	$0.030 \leq P_i \leq 0.070$	+
White spruce	457	0.019	0.005	$0.000 \leq P_i \leq 0.011$	-
Green alder	8,910	0.375	0.172	$0.138 \leq P_i \leq 0.206$	-
Willow	3,061	0.129	0.074	$0.050 \leq P_i \leq 0.098$	-
Beaked hazelnut	97	0.004	0.013	$0.003 \leq P_i \leq 0.023$	0
Low-bush cranberry	2,593	0.109	0.133	$0.102 \leq P_i \leq 0.164$	0
Red-osier dogwood	27	0.001	0.007	$0.000 \leq P_i \leq 0.014$	0
Saskatoon	29	0.001	0.001	$0.000 \leq P_i \leq 0.004$	0
Currant	314	0.013	0.019	$0.007 \leq P_i \leq 0.031$	0
Rose	2,192	0.092	0.385	$0.341 \leq P_i \leq 0.429$	+
Raspberry	178	0.007	0.031	$0.015 \leq P_i \leq 0.047$	+
Bracted honeysuckle	2,083	0.088	0.057	$0.036 \leq P_i \leq 0.078$	-
Other Species***	281	0.012	0.018	$0.006 \leq P_i \leq 0.030$	0
TOTAL	23,787	1.000	1.001		

* Bonferroni statistic indicates preference or avoidance. If the proportion falls outside of the confidence interval, a significant deviation from the expected is indicated ($P_i < 0.05$).

** Indicates whether a species was preferred (+), avoided (-), or used in proportion to its availablity (0).

*** Includes: snowberry, meadowsweet, twinning honeysuckle and mountain ash.

Table 14. Densities of principal ungulate browse species by forest age class in the Medicine Lake study area, 1982.

Browse Species	Browse Density (stems/ha)				
	Clearcut	14 yrs	30 yrs	60 yrs	80 yrs
Aspen	16,582	608	0	225	964
White birch	670	198	254	672	428
Willow	8,354	6,589	1,907	388	214
Beaked hazelnut	0	1,047	68	130	0
Low-bush cranberry	1,155	4,954	7,626	7,889	15,206
Red-osier dogwood	0	0	103	292	214
Saskatoon	330	99	86	97	964
TOTAL (15 species)	60,851	29,127	27,573	37,677	61,594

(16,582 stems/ha) of the total density of ungulate browse species in the clearcut age class. Low-bush cranberry, as a preferred browse species, was consistently available in densities exceeding 1000 stems/ha across all forest age classes. This species accounted for about 85% of the browse produced in the 80-year-old grid (Table 14). Red-osier dogwood occurred in the 30-, 60- and 80-year-old age classes but only in very low densities (less than 300 stems/ha). Beaked hazelnut, which also occurred in only three forest age classes, reached its highest density (1047 stems/ha) on open south-facing slopes in the 14-year-old sites.

The 14-year-old age class (210.41 kg/ha) yielded more than two times the amount of browse production on the clearcut areas (102.66 kg/ha) and accounted for about 64% of the total production of all species (Table 15). In contrast, the 30-, 60- and 80-year-old age classes yielded less than 41 kg/ha. Willow accounted for over 84% (177.73 kg/ha) of the total browse produced in the 14-year-old class, while regenerating aspen accounted for 76% of the total in the clearcut sites (Table 15). Although the density of browse plants in the 14-year-old age class was only about one-half the density found in the clearcut sites (Table 14), it yielded the greatest amount of ungulate browse (Table 15). This may be attributed, in part, to differences in plant age or vigor since the 14-year-old age class produced, on the average, more than four times the number of twigs per stem than the clearcut sites.

3.5.2.2 Snowshoe Hare

Density of principal snowshoe hare browse species varied markedly among age classes (Table 16). In contrast to ungulate browse densities which were highest in the youngest and oldest stands, densities of snowshoe hare browse increased with stand age. The 80-year-old age class produced 38,320 stems/ha, almost 230% more than the clearcut sites (11,605 stems/ha). Low-bush cranberry and rose densities increased to a high of 15,206 stems and 12,759 stems/ha in the 80-year-old age class.

3.5.3 Forage Production

Grasses and forbs likely contribute significantly to the summer diets of deer and elk while moose may make extensive use of leaves. Elk also may make use of

Table 15. Yield of principal ungulate browse species by forest age class in the Medicine Lake study area, 1982.

Browse Species	Browse Yield (kg/ha)				
	Clearcut	14 yrs	30 yrs	60 yrs	80 yrs
Aspen	78.14	12.13	0.00	0.08	6.89
White birch	1.09	1.75	0.57	1.33	6.54
Willow	21.55	177.73	30.74	8.32	0.14
Beaked hazelnut	0.00	7.98	0.22	0.53	0.00
Low-bush cranberry	1.72	10.44	8.54	8.91	15.60
Red-osier dogwood	0.00	0.00	0.16	0.43	0.65
Saskatoon	0.16	0.38	0.18	0.25	1.88
TOTAL	102.66	210.41	40.41	19.85	31.70

Table 16. Production of snowshoe hare browse species by forest age class in the Medicine Lake study area, 1982.

Browse Species	Browse Density (stems/ha)				
	Clearcut	14 yrs	30 yrs	60 yrs	80 yrs
White birch	670	198	254	672	428
Beaked hazelnut	0	1,047	68	130	0
Low-bush cranberry	1,155	4,954	7,626	7,889	15,206
Red-osier dogwood	0	0	103	292	214
Saskatoon	330	99	86	97	964
Currant	0	50	489	1,159	857
Rose	4,269	5,489	6,000	7,632	12,759
Raspberry	5,181	1,644	2,547	6,017	7,464
Other Species*	0	0	188	349	428
TOTAL	11,605	13,481	17,361	24,237	38,320
TOTAL (15 species)	60,851	29,127	27,573	37,677	61,594

* Includes: snowberry, buffaloberry, twinning honeysuckle, meadow-sweet and mountain ash.

fallen leaves during autumn and mild winters. To obtain some information on the availability of these types of forage among age classes, biomass sampling was conducted in Clearcut A, Clearcut B, 14, 30 and 60-year-old grids in 1981. No data concerning ungulate use of forbs and grasses were obtained.

Forb production was highest in the 30-year-old age class (889.6 kg/ha) and lowest in the one-year-old grid, while the 14-year-old grid produced the most grasses (400.6 kg/ha) (Table 8). The greatest amount of production of leaf biomass by shrubs occurred in the 14-year-old grid (Table 17). Green alder (26.49 kg/ha) and willow (18.71 kg/ha) accounted for 52% and 37% of the total biomass available on the 14-year-old grid, respectively. The 30- and 60-year-old grids yielded similar amounts of leaf biomass and were also dominated by green alder. Because the biomass sampling was conducted within nine months of clearcutting on Clearcut A and B, no data concerning leaf biomass were collected.

3.5.4 Browse Utilization

3.5.4.1 Ungulates

The amount of browse utilized by ungulates differed among forest age classes as well as between sample years (Table 18). In 1981, the highest level of browse use by ungulates occurred in the 60-year-old grid, while in 1982, browse utilization was highest in the 30-year-old age class. Overall, levels of browsing by ungulates recorded in 1982 were much lower than those observed in 1981.

Additional information on ungulate use of principal browse species was obtained by measuring the diameter of twigs at the point of browsing (DPB) and relating this to weight diameter regressions developed for each browse species. Telfer (1969) and Peek et al. (1971) have demonstrated that twig weight is closely correlated with twig diameter. Coefficients of determination (r^2) for the principal ungulate browse species in the Medicine Lake study area also showed high correlations between twig weight and twig diameter, ranging from 0.77 for white birch to 0.94 in the case of low bush cranberry (Table 19).

A comparison of DPB's recorded for each principal browse species with diameters at the base of current annual growth (DCG) indicates that ungulates are removing most of the current annual growth during the winter browsing

Table 17. Available leaf biomass (kg/ha) of shrubs by forest age class in the Medicine Lake study area, 1981.

Species	14 yrs	30 yrs	60 yrs
Aspen	0.98	0.00	0.21
Balsam poplar	0.59	0.02	0.25
White birch	0.39	0.27	0.79
Green alder	26.69	10.90	10.75
Willow	18.32	2.77	0.29
Low-bush cranberry	2.38	3.13	2.45
Red-osier dogwood	0.00	0.00	0.10
Saskatoon	0.13	0.02	0.03
Bracted honeysuckle	1.74	2.80	5.84
TOTAL	51.22	19.91	20.71

Table 18. Percent utilization of available biomass of principal browse species by ungulates and snowshoe hare by forest age class in the Medicine Lake study area, 1981 and 1982.

Species	Clearcut	14 yrs	30 yrs	60 yrs	80 yrs
1981					
Ungulates	-	5.7	15.1	39.7	-
Snowshoe Hare	-	44.6	9.9	3.8	-
1982					
Ungulates	2.8	4.1	10.6	5.2	2.5
Snowshoe Hare	4.5	13.0	14.6	16.3	0.2

Table 19. Regression statistics showing the relationship between twig weight and twig diameter for 10 browse species in the Medicine Lake study area, 1981-82.

Browse Species	Regression Equation a	b	S.E. of b	r^2	N
Aspen	-3.673	2.774	0.115	0.915	56
Balsam poplar	-3.491	2.518	0.141	0.832	66
White birch	-2.972	2.265	0.177	0.770	51
Green alder	-3.164	2.343	0.159	0.796	58
Willow	-4.003	3.092	0.121	0.904	72
Low-bush cranberry	-5.186	3.711	0.117	0.935	72
Red-osier dogwood	-4.757	3.960	0.229	0.810	73
Saskatoon	-4.077	3.457	0.183	0.790	72
Rose	-6.164	2.356	0.319	0.499	57
Bracted honeysuckle	-7.256	6.137	1.306	0.315	50

period (Table 20). Mean DPB's exceeded the mean DCG's recorded for white birch and saskatoon, indicating that at least two years growth are being browsed by ungulates. Use of older willow and red-osier dogwood growth was also evident, since the maximum DPB's recorded for these species exceeded the mean DCG's. Aspen and willow had the largest mean DCG's and mean DPB's of the principal browse species while saskatoon twigs had the smallest recorded values.

The amount of browse utilized by ungulates in each forest age class was calculated as the product of the mean weight of twigs browsed obtained from the species regression equations, stem density and the number of browsed twigs per stem for each species. Browse consumption by ungulates varied markedly among different forest age classes (Table 21). Browse utilization was highest in the clearcut and 14-year-old forest age class, where ungulates removed 4.51 kg/ha and 4.72 kg/ha, respectively. The amount of browse removed decreased to a low of 0.32 kg/ha in the 80-year-old aspen stand. On a species basis, willow was heavily utilized wherever it occurred. In the 14-year-old aspen stands, willow accounted for about 83% (3.91 kg/ha) of the biomass consumed by ungulates (Table 21).

Based on the results of the browse survey, overall levels of browse utilization by ungulates in the Medicine Lake study area are quite low. A comparison of the amount of browse consumed and the amount of browse produced annually indicates that a maximum of 5% of the current annual growth in the 30-year-old aspen stands was utilized by ungulates. About 4% of the annual browse production was used in the clearcut habitats while only 1% was utilized by ungulates in the 80-year-old stand. These data suggest that in 1982 ungulate population densities over most of the study area were well below the carrying capacity of the area. This may reflect a lower level of ungulate use in response to the severe weather conditions experienced during the winter of 1981-82.

3.5.4.2 Snowshoe Hare

As with ungulates, snowshoe hare use of the principal browse species differed among forest age classes and between sample years (Table 18). In 1981, almost 45% of the preferred browse available to snowshoe hares was browsed in the 14-year-old aspen stand. Less than 10% use was recorded for the 30- and 60-year-

Table 20. Mean diameters of current annual growth (DCG) and at point of browsing (DPB) for 10 browse species available to ungulates in the Medicine Lake study area, 1981-82.

Browse Species	DCG (mm)				DPB (mm)			
	N	$\bar{x}$	S.E.	Range	N	$\bar{x}$	S.E.	Range
Aspen	56	4.69	0.18	2.60-9.40	301	3.44	0.05	1.70-7.00
Balsam poplar	66	5.19	0.18	3.00-9.70	325	4.38	0.08	3.60-8.00
White birch	51	2.04	0.18	1.10-5.10	335	2.57	0.06	1.00-4.40
Green alder	58	4.05	0.18	1.30-7.00	329	3.62	0.10	1.60-5.50
Willow	72	3.80	0.17	1.80-7.40	426	3.46	0.06	1.40-8.60
Low-bush cranberry	72	3.56	0.16	2.00-6.90	455	2.58	0.05	1.40-5.10
Red-osier dogood	50	3.03	0.09	1.70-4.75	102	3.00	0.12	1.30-6.00
Saskatoon	47	2.32	0.08	1.25-1.30	80	2.38	0.08	1.25-4.00
Rose	57	2.74	0.07	2.70-2.90	311	2.74	0.06	1.20-4.00
Bracted honeysuckle	50	2.91	0.15	2.70-5.10	74	2.53	0.09	1.50-5.10

Table 21. Ungulate consumption of available browse biomass (kg/ha) in the Medicine Lake study area, 1981-82.

Browse Species	Clearcut	14 yrs	30 yrs	60 yrs	80 yrs
Aspen	2.32	0.16	-*	0.09	0.00
Balsam poplar	1.76	0.00	0.07	0.19	0.00
White birch	0.00	0.00	0.39	0.00	0.00
Green alder	0.00	0.09	0.14	0.00	0.00
Willow	2.18	3.91	0.85	0.00	0.00
Low-bush cranberry	0.01	0.65	0.69	0.39	0.32
Red-osier dogwood	-	-	0.14	0.00	0.00
Saskatoon	0.00	0.00	0.00	0.03	0.00
Rose	0.00	0.00	0.06	0.10	0.06
Bracted honeysuckle	0.24	0.00	0.06	0.18	0.00
TOTAL	6.51	4.81	2.40	0.98	0.38

*Species did not occur on site.

old stands. Levels of browse utilization declined markedly in 1982 as snowshoe hares entered the low phase of their population cycle. Few differences in browsing levels among the 14-, 30- and 60-year-old stands were recorded in 1982. Less than 5% of the browse species in the clearcuts showed any use by snowshoe hare and the 80-year-old aspen stand received almost no use in 1982 (Table 18).

These results indicate that during high points in their population cycle, hares may be as important a consumer of browse supplies as ungulates. This agrees with the findings of some other workers who have observed high levels of browse utilization during periods of high hare populations (Pease et al. 1979, Oldemeyer 1983). Oldemeyer (1983) noted that during the peak of a snowshoe hare cycle in Alaska, hares browsed a greater percentage of plants than did moose, removing 89.6% of the total browse production.

Oldemeyer (1983) also reported a high degree of overlap in species selected for browsing by moose and hares. Browse production in his Kenae study area was dominated by a single species however. Paper birch produced an average of 102 kg/ha while willow and aspen together comprised another 3.7 kg/ha. Less overlap was observed during the present study, perhaps reflecting the greater diversity of browse species in Alberta aspen stands. None of the four species preferred ($P < 0.05$) by ungulates were also selected preferentially by snowshoe hares. Neither were the three species preferred by hares selected preferentially by ungulates. Willow, which was a major ungulate browse species, was avoided by hares and rose, which was a principal browse species for hares, was essentially not utilized by ungulates. The greatest amount of dietary overlap occurred in the case of low-bush cranberry, which was preferred as ungulate browse and used in proportion to availability by hares. Cranberry was the most abundant browse species overall and was available within the vertical browsing range of both hares and ungulates.

3.6 WILDLIFE USE IN RELATION TO FOREST AGE CLASS

3.6.1 Ungulates

Moose, elk, white-tailed deer and mule deer are known to occur within the Medicine Lake study area. Overall, results of the pellet group surveys indicate that moose are the most abundant ungulate species in the study area, followed by deer and elk (Table 22). The pellet group counts also indicated that there were pronounced differences in ungulate use between sample years and among the different forest age classes.

On average, moose and deer pellet group densities declined approximately 50% and 82%, respectively, from 1981 to 1982 while elk pellet densities decreased only 19% (Table 22). This marked decline in relative habitat use by ungulates over the two sample years was likely associated with the unusually severe weather conditions during the 1981-82 winter. Winter conditions during 1980-81 were considerably milder than the long-term normals for the region, however this situation was completely reversed the following winter (Figure 7). Month-end snow depths ranged from 50 cm in January to 47 cm in March 1982, while mean month-end temperatures were approximately 10°C below the long-term normals. This combination of deep snow and cold temperatures probably resulted in a shift of ungulate use from aspen-dominated habitats to those areas supporting higher densities of coniferous vegetation.

Significant differences in ungulate use of forest age classes were also apparent (Table 23). In 1981, habitat use by moose was not significantly different ($P > 0.05$) between the 14- and 30-year-old aspen stands. However, the 60-year-old stand received significantly less ($P < 0.05$) use by moose than the 14- and 30-year-old stands. In contrast, elk use increased with stand age, with the highest density recorded in the 60-year-old stand. No significant differences ($P > 0.05$) in deer use were detected among the three forest age classes (Table 23).

Significant differences in use of the different forest age classes by moose and elk were also recorded in 1982 (Table 23). Moose again made the greatest use of the 14- and 30-year-old stands with use declining to age 60, before increasing again slightly to the 80-year-old stand. Although moose made little use of the clearcut areas, higher pellet group densities were associated with the forest edge

Table 22. Densities of ungulate pellet groups (No./ha) by forest age class in the Medicine Lake study area.

	Clearcut	Forest Edge	14 yrs	30 yrs	60 yrs	80 yrs	Study Area
1981							
Moose	-	-	85.5	76.0	43.0	-	65.1
Deer	-	-	61.8	77.0	50.0	-	63.1
Elk	-	-	7.3	16.0	30.0	-	19.6
No. of Plots	-	-	110	100	100	-	310
1982							
Moose	1.7	25.9	95.7	37.0	18.5	26.0	32.6
Deer	17.2	12.1	13.0	13.0	6.5	10.0	11.2
Elk	60.3	43.1	2.9	6.7	18.0	7.0	15.9
No. of Plots	58	58	138	300	200	100	796

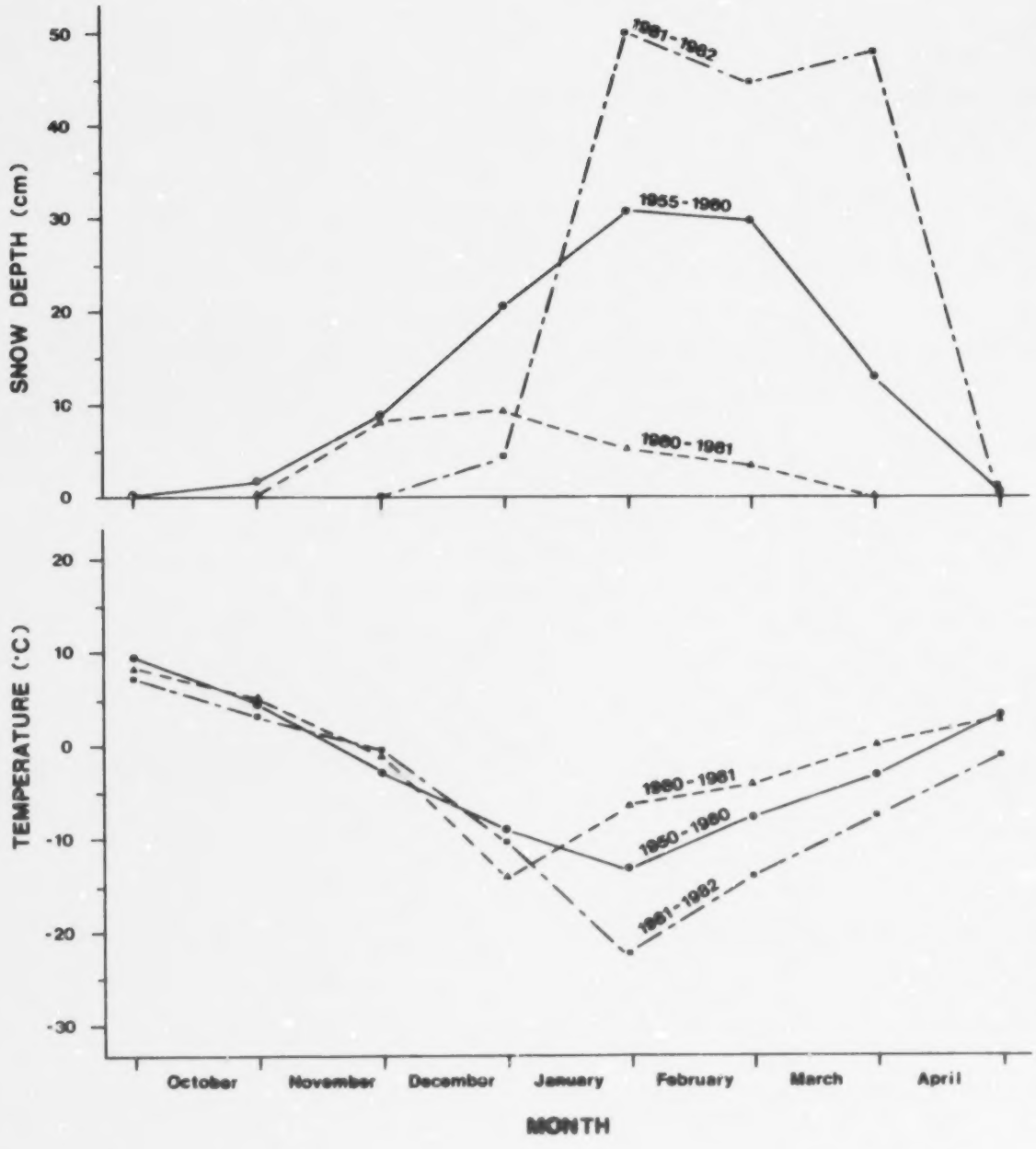


Figure 7. Comparison of winter climatic conditions in the Rocky Mountain House area during 1980-81 and 1981-82 with long-term climatic normals (data from Environment Canada).

Table 23. Comparisons of mean pellet groups per plot ($\bar{x} \pm$ S.E.) for moose, deer and elk by forest age class in the Medicine Lake study area.

	Overall Difference	Clearcut		Forest Edge		14 yrs		30 yrs		60 yrs		80 yrs	
		$\bar{x}$	± S.E.	$\bar{x}$	± S.E.	$\bar{x}$	± S.E.	$\bar{x}$	± S.E.	$\bar{x}$	± S.E.	$\bar{x}$	± S.E.
1981													
Moose	P< 0.05					0.86^{a}	0.10	0.76^{a}	0.05	0.43^{b}	0.19		
Deer	NSD					0.62	0.12	0.77	0.15	0.50	0.10		
Elk	P < 0.01					0.08^{a}	0.02	0.16^{b}	0.02	0.30^{c}	0.04		
No. of Plots						110		100		100			
1982													
Moose	P < 0.01	0.02^{a}	0.02	0.26^{ac}	0.05	0.48^{b}	0.07	0.37^{b}	0.04	0.19^{a}	0.03	0.26^{c}	0.05
Deer	NSD	0.17	0.07	0.12	0.04	0.07	0.02	0.13	0.03	0.07	0.02	0.10	0.03
Elk	P < 0.01	0.61^{a}	0.11	0.43^{d}	0.06	0.01^{b}	0.01	0.07^{bc}	0.01	0.18^{c}	0.03	0.07^{b}	0.03
No. of Plots		58		58		138		300		200		100	

Note: Mean values with different superscripts are significantly different (P < 0.05).

zones adjacent to the clearcut areas (Table 23). Habitat use by elk was greatest in areas associated with clearcutting. The highest pellet group densities were associated with the clearcuts and the edges between clearcut and aspen forests. Within forested habitats, elk use increased from 14- to 60-year-old stands but decreased in the 80-year-old age class (Table 23). Although deer densities were highest in the clearcut and forest edge habitats, no statistically significant differences ($P > 0.05$) in deer use of forest age classes were observed.

3.6.2 Snowshoe Hare

Habitat use by snowshoe hares differed significantly with respect to forest age class (Table 24). In 1981, pellet densities were highest in the 14-year-old stands and lowest in the 60-year-old stand. Densities were also highest on the 14-year-old aspen stands in 1982, although the 30-year-old stands had a lower density than the 60-year-old stand. Hares did not use the 1- and 2-year-old clearcuts and made very little use of the 80-year-old stand. As with ungulate pellet group densities, habitat use by snowshoe hares declined markedly between 1981 and 1982.

The lack of correlation between pellet densities and browse availability (Table 16) in the various sample stands suggests that factors other than browse availability were having an overriding influence on hare distribution and habitat use. Other studies have shown that hare distribution is closely associated with areas containing a high density of cover in the tall shrub layer (Van Camp and Telfer 1975, Conroy et al. 1979, Wolff 1980, Wolfe et al. 1982, Pietz and Tester 1983). Cover apparently is required both as shelter and protection from predators. Van Camp and Telfer (1975) reported a very high correlation between hare use and density of the tall shrub-sapling layer. They obtained a coefficient of determination (R^2) of 0.79 between hare use and both the number of stems taller than 42 inches (107 cm) and the product of stem density and mean crown volume of stems.

The high densities of hare pellets in the 14-year-old stand therefore appears to be related to cover provided by well-developed, tall shrub layer. Cover values for the tall shrub strata were highest in the 14-year-old stands, progressively declining as the forest matured (Table 6). Because of the snow cover, the low

Table 24. Comparisons of mean pellet groups per plot ($\bar{x} \pm$ S.E.) for snowshoe hare by forest age class in the Medicine Lake study area.

	Overall Difference	Clearcut		Forest Edge		14 yrs		30 yrs		60 yrs		80 yrs	
		$\bar{x}$	± S.E.	$\bar{x}$	± S.E.	$\bar{x}$	± S.E.	$\bar{x}$	± S.E.	$\bar{x}$	± S.E.	$\bar{x}$	± S.E.
1981	$P < 0.05$					19.28^a	2.38	2.27^b	0.56	0.71^b	0.19		
No. of Plots						110		100		100			
1982	$P < 0.05$	0.00^a		0.93^a	0.27	8.04^b	0.01	2.93^c	0.23	4.58^c	0.76	0.02^a	0.01
No. of Plots		58		58		138		300		200		100	

Note: Mean values with different superscripts are significantly different ($P < 0.05$).

shrub layer and ground cover have limited value as cover for hares during winter. This is apparently reflected in the low hare use observed on the clearcut areas and in the 60- and 80-year-old stands where cover values for the low shrub layer were relatively high but tall shrub cover was lacking. The high density of deadfall in the 14-year-old stands provided additional cover for hares thereby contributing to the high hare densities supported by these stands.

3.7 SNAGS AND DEADFALL

As a forest matures, natural processes and a variety of agents cause mortality of individual trees. Forest fires sometimes cause widespread tree mortality, killing all or a portion of the trees in a stand. The dead trees often remain standing for many years before the combined action of decay and wind causes them to fall to the forest floor. Both standing dead trees (snags) and dead and downed woody material (deadfall) represent a unique habitat component that is essential for certain species of birds and mammals. Because this habitat component tends to be associated with a distinctive group of wildlife species, we have dealt with it as a separate section of the report.

3.7.1 Causes of Aspen Mortality

A number of factors or agents can cause mortality of aspen trees and contribute to snag and deadfall formation. Natural mortality agents include suppression, disease, insects, flooding and age, while man-induced mortality of aspen may result from fires and mechanical disturbances.

In the Medicine Lake study area, fire and suppression appeared to be the major mortality agents influencing snag development (Table 25). Approximately 91.0% of the snags inventoried in the 14-year-old age class showed evidence of fire scars. In spite of the relatively low flamability of aspen stands (Ohmann et al. 1978), fire is a major mortality agent in Alberta. Crown fires are rare in aspen stands except under extremely dry conditions, however the litter provides a hot, fast-burning ground fuel (Alberta ENR 1979). In addition, many fires in aspen stands in Alberta result from their proximity to the more combustible coniferous stands. The lower flamability of aspen stands appears to have an important bearing on subsequent habitat development. Burning is frequently incomplete, leaving remnant stands of live or partially live trees. As well, mortality may occur before heart rot is pronounced, consequently snags may remain standing for a relatively long period of time.

Suppression was the only other mortality factor which contributed significantly to snag development in the Medicine Lake study area, accounting for approximately 77% of the snags encountered in the 30-year-old stands (Table 25). The effects of suppression on aspen gradually declined to a low in the 80-year-old

Table 25. Mortality factors contributing to snag development in different age classes in the Medicine Lake study area, 1981-82.

Mortality Factor	Percent of Total			
	14 yrs	30 yrs	60 yrs	80 yrs
Fire	91.0	3.5	8.1	0.0
Disease	3.2	1.0	1.3	5.4
Age	0.0	0.4	5.0	8.9
Suppression	0.0	75.6	56.9	22.0
Insects	0.0	2.2	1.8	5.4
Unknown	5.8	17.3	26.9	58.3
TOTAL		100.0	100.0	100.0

class. Anderson and Anderson (1968) reported that suppression and disease are the principal mortality agents in young aspen stands. As a stand matures, competition from older, dominant trees for light, water and nutrients causes natural mortality of the younger and smaller trees.

A number of diseases also kill aspen, however the influence of disease in snag formation within the Medicine Lake area was not always readily apparent (Table 25). Hypoxylon canker, caused by the fungus **Hypoxylon pruinatum**, is one of the most important pathological agents of aspen (Baranyay 1967, Anderson and Anderson 1968, Perala 1977, Ohmann et al. 1978). Hypoxylon canker is the most important potential pathogen of aspen stands managed on a short (35 yr) rotation, killing an average of 1-2% of the trees in a stand annually (Ohmann et al. 1978). This fungal disease kills aspen trees by invading and girdling the bark and outer stem tissues (Anderson and Anderson 1968). Baranyay (1967) reported that infection usually occurs through dead branch stubs, although entry can also occur through wounds caused by insects, fire, frost cracks, sun scald, animal damage, or mechanical damage (Graham and Harrison 1954, Hinds and Krebiel 1975).

Although hypoxylon canker also affects older trees, the major mortality agent in mature or overmature stands is heart rot (Perala 1977). The most serious form of decay is **Fomes igniarus** which is responsible for about 35% of the decay in aspen stands (Steneker 1976). The decay usually enters the tree through dead branch stubs and wounds, initially staining and later decaying the heartwood (Steneker 1976, Perala 1977). Advanced decay can be detected by the presence of gray conks on the stem, which are the fruiting bodies (sporophores) of **F. igniarus**. Tree mortality often occurs as a result of structural weakening of the stem and subsequent blowdown (Anderson and Schipper 1978). While **F. igniarus** appears to be the most serious decay, other agents including **Corticum polygonium** and **Radulum caeserium** may also be important.

Although over 300 species of insects feed on aspen, only a few are considered capable of causing significant damage (Ohmann et al. 1978). The most important defoliators of aspen in western Canada are the forest tent caterpillar (**Malacosoma disstria**) and the large aspen tortrix (**Choristoneura conflictana**) (Steneker 1976). The forest tent caterpillar exhibits widespread outbreaks at 6

to 16-year intervals (Ohmann et al. 1978). It causes little direct mortality of trees but results in a pronounced decrease in growth during the period of infestation (Perala 1977, Steneker 1976). The large aspen tortrix is also capable of undergoing spectacular outbreaks but heavy infestations seldom last more than 1 or 2 years (Ohmann et al. 1978). A heavy infestation by forest tent caterpillars occurred in the Medicine Lake area during 1981 and 1982.

Other insects which may cause significant damage to aspen are the gray willow-leaf beetle (**Galerucella decora**), the aspen leaf beetle (**Chrysomela crotchi**) and the poplar borer (**Saperda calcarator**) (Davidson and Prentice 1968). The tunneling activity of the large larvae of the poplar borer may contribute to mortality by weakening trees (Ohmann et al. 1978) or providing infection courts for pathogens (Perala 1977).

3.7.2 Relative Abundance and Physical Characteristics of Snags and Deadfall by Forest Age Class

The abundance and physical characteristics of snags and deadfall were determined using transect surveys on each of the 10 study grids. The physical characteristics included features that other workers have reported to be important as factors influencing wildlife use. These included the height, diameter, proportion of remaining limbs, proportion of remaining bark, the type of top (broken or pointed) and the extent of decay. Decay was subjectively evaluated by rating the condition of the sapwood as hard or soft. On soft snags and deadfall the wood usually yielded easily when struck with an axe or other hard object.

Both the density (Table 26) and physical characteristics (Table 27) of snags varied significantly ($P < 0.01$) among the differently aged aspen stands. No snags were encountered in the clearcut areas because all standing vegetation was harvested in 1981. While there was no apparent trend in densities of hard snags among the differently aged aspen stands, the relative abundance of soft snags tended to increase as stands matured, with the highest density (363 snags/ha) occurring in the 80-year-old stand (Table 26). Overall, soft snags were more abundant in the study area than hard snags. Average height and the percentage of bark remaining on hard and soft snags also tended to increase with stand maturity, however snag size and the percentage of broken limbs were significantly greater ($P < 0.01$) in the 14-year-old aspen stands (Table 27).

Table 26. Comparison of snag densities in aspen stands of different ages with respect to level of decay and snag origin.

	Snag Density (No/ha)			
	14 yrs	30 yrs	60 yrs	80 yrs
Decay Category				
Hard	22	267	236	248
Soft	229	314	352	363
Origin				
Current	13	557	538	611
Remnant	238	24	50	0

Table 27. Physical characteristics of snags in aspen stands of different ages in the Medicine Lake study area.

Variable	Overall Difference	14 yrs		30 yrs		60 yrs		80 yrs	
		x	S.E.	x	S.E.	x	S.E.	x	S.E.
HARD SNAGS									
Snag height (m)	$P < 0.01$	6.0^{a}	1.4	10.2^{b}	0.3	10.5^{b}	0.4	17.7^{c}	0.7
Snag DBH (cm)	$P < 0.01$	12.4^{a}	1.1	7.4^{b}	0.3	9.6^{c}	0.5	19.5^{d}	0.6
Limbs broken (%)	$P < 0.01$	66.4^{a}	10.5	48.1^{bc}	2.0	41.5^{b}	2.9	54.6^{c}	3.6
Bark Remaining (%)	$P < 0.01$	92.5^{a}	2.6	92.7^{a}	0.7	94.3^{a}	0.8	99.1^{b}	0.3
SOFT SNAGS									
Snag height (m)	$P < 0.01$	3.2^{a}	0.2	6.7^{b}	0.7	5.5^{c}	0.3	10.7^{d}	0.7
Snag DBH (cm)	$P < 0.01$	16.2^{a}	0.7	8.4^{b}	0.4	12.0^{c}	0.7	16.6^{a}	0.5
Limbs broken (%)	$P < 0.01$	96.0^{a}	1.1	69.6^{b}	2.0	78.6^{c}	2.0	85.3^{c}	2.3
Bark remaining (%)	$P < 0.01$	53.6^{a}	2.7	77.7^{b}	1.7	72.5^{b}	2.2	87.2^{c}	1.7

Note: Mean values with different superscripts are significantly different ($P < 0.05$).

The high density and large average size of soft snags in the 14-year-old aspen stands appears to be related to stand origin (Plate 4). Since the 14-year-old aspen stands were of fire origin, many of the soft snags that were inventoried would not normally occur after an area was clearcut. Therefore, density estimates for soft snags are greater than expected in a 14-year-old stand of clearcut origin.

The results of the deadfall survey indicate that the relative abundance of deadfall less than 10 cm in diameter is highest following clearcutting operations, but then declines as the stands mature to 60 years of age (Table 28). At 80 years of age, small pieces of deadfall tend to accumulate on the forest floor through overmaturity of trees, blowdown and other mortality factors. Densities of deadfall greater than 10 cm in diameter are considerably lower than the smaller pieces of deadfall. Maximum densities of deadfall greater than 10 cm diameter were reached at 80 years of age (27.6/100 m) while low densities were associated with the clearcut, 30- and 60-year-old aspen stands (Table 28). The largest mean diameter (19.1 cm) of deadfall greater than 10 cm diameter occurred in the 30- and 60-year-old stands, however deadfall reached its highest point above ground (13.4 cm) in the 80-year-old aspen stand. The condition of deadfall was associated with various stages of decay and deterioration which differed across forest age classes (Table 29). The clearcut and 14-year-old stands were typified by hard pieces of deadfall with either most or little of the bark remaining, while the majority of deadfall encountered in the 30- and 60-year-old stands were in the advanced stages of decay. About 70% of the deadfall inventoried in the 80-year-old stand was comprised of hard deadfall similar to that found in the clearcut and 14-year-old aspen stands (Table 29).

3.7.3 Wildlife Use of Snags

In the Medicine Lake study area, 23 avian and 9 mammalian species may utilize snags for nesting, roosting, denning, hibernating, shelter or foraging (Appendix VII and XI). However little field information regarding snag use by mammals was collected. Of the 23 avian species, only eight species were relatively common in the area. These species comprised two major groups: (a) those species that excavate their own cavities (cavity excavators) and (b) those species that occupy natural cavities or cavities abandoned by other bird species

Plate 4. Remnant snags such as this one in a 14-year-old stand are an important feature of fire successional aspen stands. Snags provide nesting sites and foraging substrates for a variety of snag-dependent wildlife species.

Table 28. Characteristics of deadfall in aspen stands of different ages in the Medicine Lake study area, 1982.

Deadfall Characteristics	Clearcut	14 yrs	30 yrs	60 yrs	80 yrs
Abundance (No./100 m)					
<10 cm dbh	90.4	52.2	46.7	25.8	41.6
>10 cm dbh	4.2	16.8	6.5	4.5	27.6
Mean Diameter (cm)*	16.9	15.7	19.1	19.1	14.5
Height Above Ground (cm)*	1.1	11.6	3.3	5.6	13.4

*Measurements pertain to large (>10 cm diam) deadfall component.

Table 29. Condition of deadfall in different age classes in the Medicine Lake study area, 1982.

Condition Class*	Percent of Total				
	Clearcut	14 yrs	30 yrs	60 yrs	80 yrs
1	54.3	4.8	8.1	14.1	29.0
2	22.9	59.2	16.5	10.1	40.5
3	1.4	0.8	1.3	7.5	6.1
4	4.3	14.9	12.9	5.2	4.6
5	17.1	20.3	61.2	63.1	19.8
Total	100.0	100.0	100.0	100.0	100.0

* 1 Hard, most bark remaining,
2 Hard, little bark remaining,
3 Soft, most bark remaining,
4 Soft, little or no bark,
5 Advanced decay, moss covered and/or sloughing heartwood.

(cavity dependent). The former group includes the pileated woodpecker, hairy woodpecker, common flicker, yellow-bellied sapsucker and the black-capped chickadee. The later group consists of three species and includes the red-breasted nuthatch, house wren and the tree swallow. Both chickadees and nuthatches are capable of excavating their own nest cavities in decayed snags but often use natural cavities or cavities excavated by other species.

Many recent studies of snag dependent birds have been conducted in either the eastern hardwood forests or in the western larch-Douglas fir forests (Table 30). Because of the general paucity of information concerning bird use of snags in aspen forests, extrapolation of results from studies of different forest cover types to aspen stands may create misleading impressions on factors influencing snag use. For example, the minimum snag sizes reported to be of use to snag dependent birds are sometimes larger than the mean size of mature aspen. Nevertheless, it appears that bird use of snags is influenced by at least three major physical characteristics of the snag itself: diameter, height and condition.

The importance of snag diameter and height for nesting and feeding has been documented by numerous researchers. Conner et al. (1975) found that the size of the woodpecker dictated the size of the nest tree used. Pileated woodpeckers generally preferred the largest diameter trees and nested at greater heights above ground than did the smaller woodpeckers. Similarly, Mannon et al (1980) reported that of the various snag characteristics tested, a positive correlation existed only between densities of hole nesting birds and mean snag diameter. Raphael and White (1984) found that snag diameter was the most important discriminator between nest and non-nest snags.

Flack (1976), in his study of bird populations of aspen forests in western North America, noted that densities of woodpeckers increased abruptly in areas supporting snags that were at least 15 cm in diameter. By using this diameter as one index of snag suitability for cavity excavators and cavity dependent species in boreal aspen stands, some indication of snag formation and bird use in differently aged stands may be obtained. The density of snags greater than 15 cm in diameter showed a general increase with age (Figure 8). As densities of live trees declined to 60 years of age, there was an increase in the number of snags. The relative abundance of cavity excavators and cavity dependent birds

Table 30. Comparison of bird use of snags in four different forest cover types.

Species	Forest Type	Snag dbh (cm)		Min.	Reference
		x̄	Range		
Common flicker	Douglas fir	61	36-112	36	Mannan et al. 1980
	Oak-hickory	37	30-46	30	Connor et al. 1975
	Western larch-Douglas fir	53	25-130	25	McClelland et al. 1979
	Aspen	40	25-64	25	Flack 1976
Pileated woodpecker	Douglas fir	78	46-172	46	Mannan et al. 1980
	Oak-hickory	55	33-91	33	Conner et al. 1975
	Western larch-Douglas fir	81	58-104	58	McClelland et al. 1979
Yellow-bellied sapsucker	Douglas fir	101	56-216	56	Mannan et al. 1980
	Western larch-Douglas fir	58	23-119	23	McClelland et al. 1979
	Aspen	30	23-46	23	Flack 1976
Hairy woodpecker	Douglas fir	92	48-172	48	Mannan et al. 1980
	Oak-hickory	41	20-64	20	Conner et al. 1975
	Western larch-Douglas fir	36	23-74	23	McClelland et al. 1979
	Aspen	29	20-41	20	Flack 1976
Downy woodpecker	Oak-hickory	32	15-66	15	Conner et al. 1975
	Western larch-Douglas fir	25	18-36	18	McClelland et al. 1979
	Aspen	25	15-30	15	Flack 1976
Black-capped chickadee	Western larch-Douglas fir	20	10-30	10	McClelland et al. 1979
Red-breasted nuthatch	Douglas fir	118	74-185	74	Mannan et al. 1980
	Western larch-Douglas fir	53	10-89	10	McClelland et al. 1979

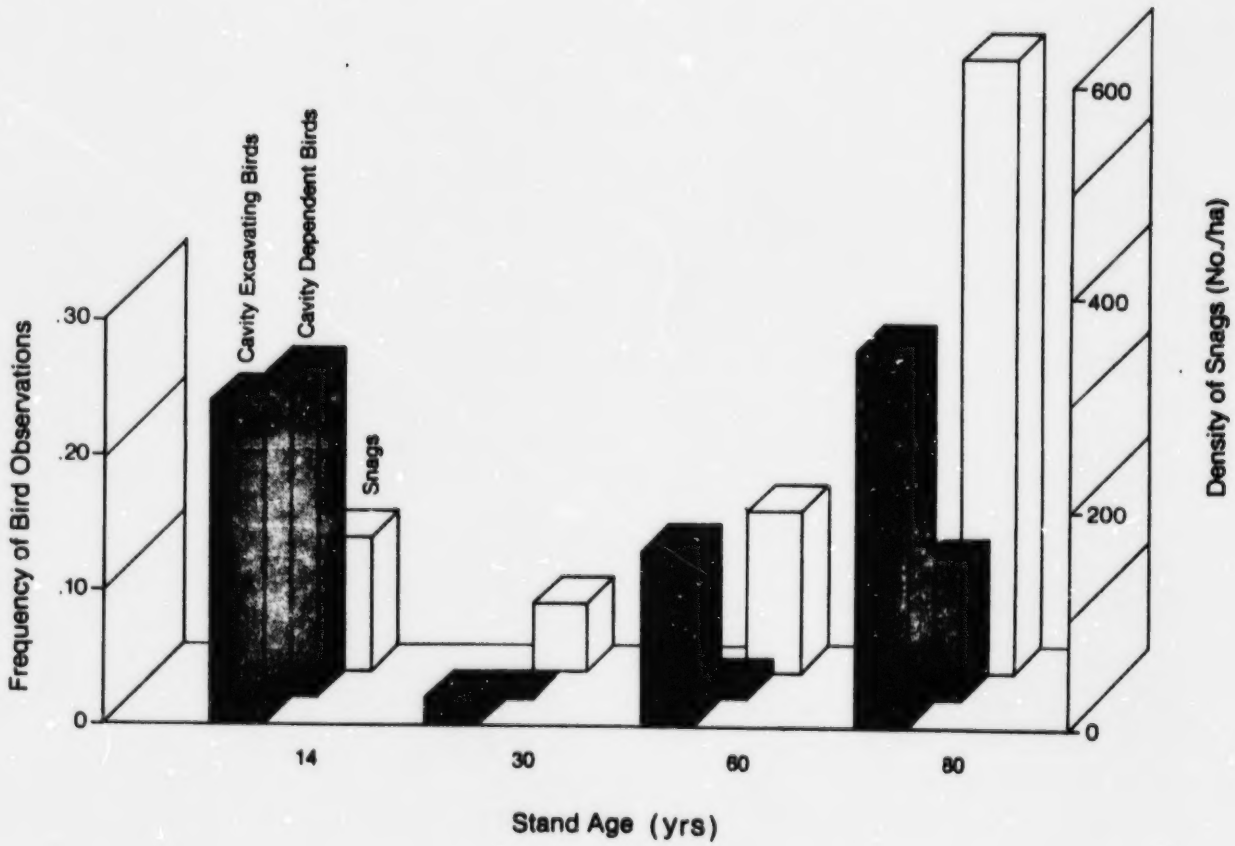


Figure 8. Habitat use by cavity excavating and cavity dependent birds in aspen stands of different ages in relation to density of large (> 15 cm dbh) snags. Habitat use is based on the mean number of bird observations at each sample station.

also increased with age and with snag density, reflecting the increased suitability of the aspen stands for nesting, roosting and foraging. The presence of relatively high densities of remnant snags from the previous stand undoubtedly influenced woodpecker use of the 14-year-old stands (Figure 8). Because of incomplete burning, these remnant stands of dead and partially dead veteran trees remained standing and subsequently influenced habitat development and habitat use of the 14-year-old age class.

In the present study, only 10 nest cavities were located during the snag survey (Table 31). No attempt was made to distinguish active or inactive nests and therefore, it is not known whether the nests had been used during the previous breeding season or had been abandoned for some time. All of the nests were associated with soft snags ranging in size from 8.0 cm to 32.0 cm in diameter ($\bar{x}$ = 18.3 cm dbh) (Table 31). The majority of snags were aspen stems which occurred in the 14-year-old age class. About 82% of the snags had broken tops and therefore averaged only 4.8 m in height. In contrast, aspen snags with intact tops exceeded 9.0 m in height (Table 31). Apparently the presence of a broken top on a snag is an important prerequisite for cavity excavators since it provides an entry point for fungal heart rot (McClelland et al 1979; Mannon et al. 1979; Kilham 1971; Rapael and White 1984). The resulting decay and deterioration of the snag creates soft heartwood and hard sapwood, providing ideal conditions for cavity excavators (Scott 1977, Mannon et al 1977). In the present study about 89% of the nest cavities were located within 1.0 m of a broken top.

Overall, densities of cavity excavators and cavity-dependent bird species were low in the Medicine Lake study area. Black-capped chickadees, red-breasted nut hatches, house wrens and yellow-bellied sapsuckers were among the more common species. Although these low densities may reflect in part, low snag densities and hence poorer habitats, the major reasons may be related to the autecology of aspen.

Flack (1976) offers a convincing explanation for the low number of cavity nesting bird species in the aspen forests of western Canada. He notes that use of trees by woodpeckers for nesting is limited until trees reach a dbh of at least 15 cm (6 in). It may take an aspen tree 30-40 years to reach this size (Maini and Cayford 1968). In the absence of disturbance, aspen forests in western Canada

Table 31. Characteristics of nests found in soft snags in the Medicine Lake study area, 1981-82.

Tree Species	Age Class	DBH (cm)	Snag Height (m)	Cavity Height (m)	Top of Snag
Unknown	14	17.0	5.0	4.6	Broken
Aspen	14	10.5	4.0	3.5	Broken
Aspen	14	8.0	9.0	4.0	Intact
Aspen	14	10.0	9.5	4.0	Intact
Aspen	14	11.5	1.5	1.0	Broken
Balsam Poplar	30	32.0	6.5	5.5	Broken
Balsam Poplar	30	32.0	6.5	6.0	Broken
Aspen	30	25.0	2.0	1.9	Broken
Willow	60	15.0	10.0	3.0	Broken
Aspen	60	22.0	4.5	3.7	Broken

typically have a life span of approximately 65–80 years (Maini and Cayford 1968). This is apparently considerably shorter than in the western United States where decay is less pronounced and trees live 80–100 years (Flack 1976). Consequently, even in the absence of disturbance there is a relatively short period of time available for cavity excavators and cavity dependent birds to colonize and exploit aspen forests.

In actuality, this period is further shortened by a number of disturbance factors that affect aspen forests in western Canada. In the parkland region climatic fluctuations and agricultural practices have had a major influence on aspen forests (Bird 1961). In the boreal mixedwood region, forest fires have likely been the major influence. Wildfires ignited by summer thunder storms periodically burn large areas in the forested region of Alberta. As a result, many aspen stands do not reach mature or overmature seral stages, and the period of time for which suitable habitat is available for cavity nesters is further limited. Although fire suppression efforts have greatly reduced the frequency of forest fires during the past two decades, fires remain a major factor influencing successional development and wildlife use of aspen forests.

3.7.4 Wildlife Use of Deadfall

Downed woody material continues to be used as a foraging substrate by many of the bird species that feed on sangs. In addition, a number of other species of birds and mammals use deadfall for nesting, denning, breeding, foraging or cover. In the Medicine Lake area the list of species that use deadfall includes 14 species of birds (Appendix VII) and 12 species of mammals.

During the transects surveys on the 10 study grids, each piece of deadfall that intersected a transect was carefully examined for evidence of wildlife use. Some types of use were readily apparent, however the majority of use did not result in obvious sign and therefore was not detected. For example, use of deadfall as a foraging substrate by gleaners is difficult to detect. Similarly, use by small mammals is usually not apparent. Workers who have been involved in small mammal livetrapping studies are aware of the use made of deadfall as cover and travel corridors by mice, voles and shrews. Deadfall also provides a foraging substrate for insectivorous mammals such as the masked shrew, pygmy

shrew and deer mouse and for primarily herbivorous mammals such as the red-backed vole which feeds on mosses or saprophytes.

Because of the limited data regarding wildlife use of large deadfall (>10 cm dbh), all of the use data were grouped according to use category rather than by forest age class. Of the 153 instances of wildlife use of deadfall recorded, three major use types represented approximately 99% of the total (Table 32). These included bear diggings, recent woodpecker feeding sites and shelter or denning areas for snowshoe hare (Table 32).

Bear diggings typically occurred in and around Class 4 and 5 deadfall which averaged about 18 cm in diameter (Table 32). Most of this type of deadfall was in the ground or partially buried. Class 4 and 5 deadfall is in an advanced stage of decay where it is moss covered and may or may not be characterized by sloughing heartwood. The wood is therefore soft and has little or no bark cover. This undoubtedly creates ideal habitat conditions for grubs, ants and other wood-boring insects on which bears feed.

Although the size of deadfall used by woodpeckers for foraging was identical to that used by bears, feeding activity was generally restricted to Class 2 deadfall. However evidence of woodpecker feeding was observed on all classes of deadfall. Class 2 deadfall is characterized by hardwood with little or no bark remaining.

Deadfall appeared to be an important habitat component for snowshoe hares, particularly on the 14-year-old grids (Plate 5). In addition to providing cover from avian and mammalian predators, deadfall was often used as a platform for extending the vertical feeding range of hares and it appears to have been important for thermal shelter. During winter, shelters or burrows were often situated in the snow-free space under deadfall. A dense deadfall layer effectively traps an insulating snow cover providing subnivean shelter for hares and other small mammals. The physical characteristics of deadfall used by hares for shelter and burrows are indicated in Table 32. In both cases deadfall was of relatively large diameter, however deadfall that was supported at a greater height above ground received more use as shelter or cover. Also, deadfall used for shelter or burrows was usually hard; 62% of the shelters and 61% of the burrows recorded were associated with deadfall in condition Class 2.

Table 32. Wildlife use of deadfall (greater than 10 cm dbh) in the Medicine Lake study area 1982.

Types of Wildlife Use	N	DBH (cm)			Height Above Ground (cm)		
		x	S.E.	Range	x	S.E.	Range
Bear Digging	47	21.8	1.3	12-54	3.3	1.4	0-25
Woodpecker Feeding	34	18.6	1.2	11-48	8.9	2.5	0-48
Hare Shelter	37	16.4	0.5	11-48	18.0	2.1	5-48
Hare Burrows	20	17.9	1.2	11-30	2.1	2.1	0-41

Plate 5. Deadfall provides denning sites (A) and cover (B) for smaller mammals such as the snowshoe hare.

It appears then that, as was the case with snags, tree size (diameter) is an important factor affecting use of deadfall by wildlife. Mean diameters for the uses described here ranged from 16.4 to 21.8 cm. Trees of this size only develop in stands older than 40 years. It also appears that the uses of deadfall change with age. Hard deadfall is more important for cover or shelter, while soft, decayed deadfall becomes more important as a source of food.

4.0 DISCUSSION

4.1 EFFECTS OF SHORT ROTATION MANAGEMENT ON WILDLIFE

4.1.1 Changes in Habitat Structure and Composition

The results of the present study indicate that pronounced differences in wildlife use exist among aspen stands of different ages in the Medicine Lake area. For most species these differences are more a function of changing habitat structure as the stands mature than changes in vegetation composition. Along with the increase in structural diversity as a stand progresses from the herbaceous-shrub stage to the mature and old growth stages, the interactive effects of the major vegetation strata on sunlight penetration and moisture accumulation cause changes in the microclimatic conditions in aspen forests.

The changes in structure of aspen forests as they progress through the major successional stages is summarized in Figure 9. One or two-year-old clearcuts are structurally simple habitats characterized by a well-developed ground cover dominated by grasses and the absence of a woody canopy cover. Following conventional logging operations, clearcut areas usually contain a large amount of residual woody material comprised of the tops of trees, cull trees, shrubs, and unmerchantable tree species that are left standing. During biomass harvesting however, these components would be utilized, leaving a forest floor devoid of large diameter snags or downed woody material. Full tree harvesting operations on the two clearcut areas sampled at Medicine Lake resulted in the recovery of 85-95% of the total available biomass which included trees and shrubs as small as 4 cm dbh (Coban Institute 1981). Based on a study of several small watersheds in Alberta, Hillman (1983) demonstrated that clearcutting resulted in increased snow accumulation, which along with the reduced transpiration resulting from tree removal, caused a significant increase in soil moisture levels. On the Medicine Lake clearcut plots the increase in moisture availability resulted in ponding of surface water in low areas in spring, creating temporary habitat for several species of semi-aquatic bird species and amphibians.

As regenerating stands reach the sapling stage at around age 10-15, a well-developed tall shrub layer comprised of young aspen, alder and willow is the most prominent structural characteristic. Increased shading and competition causes

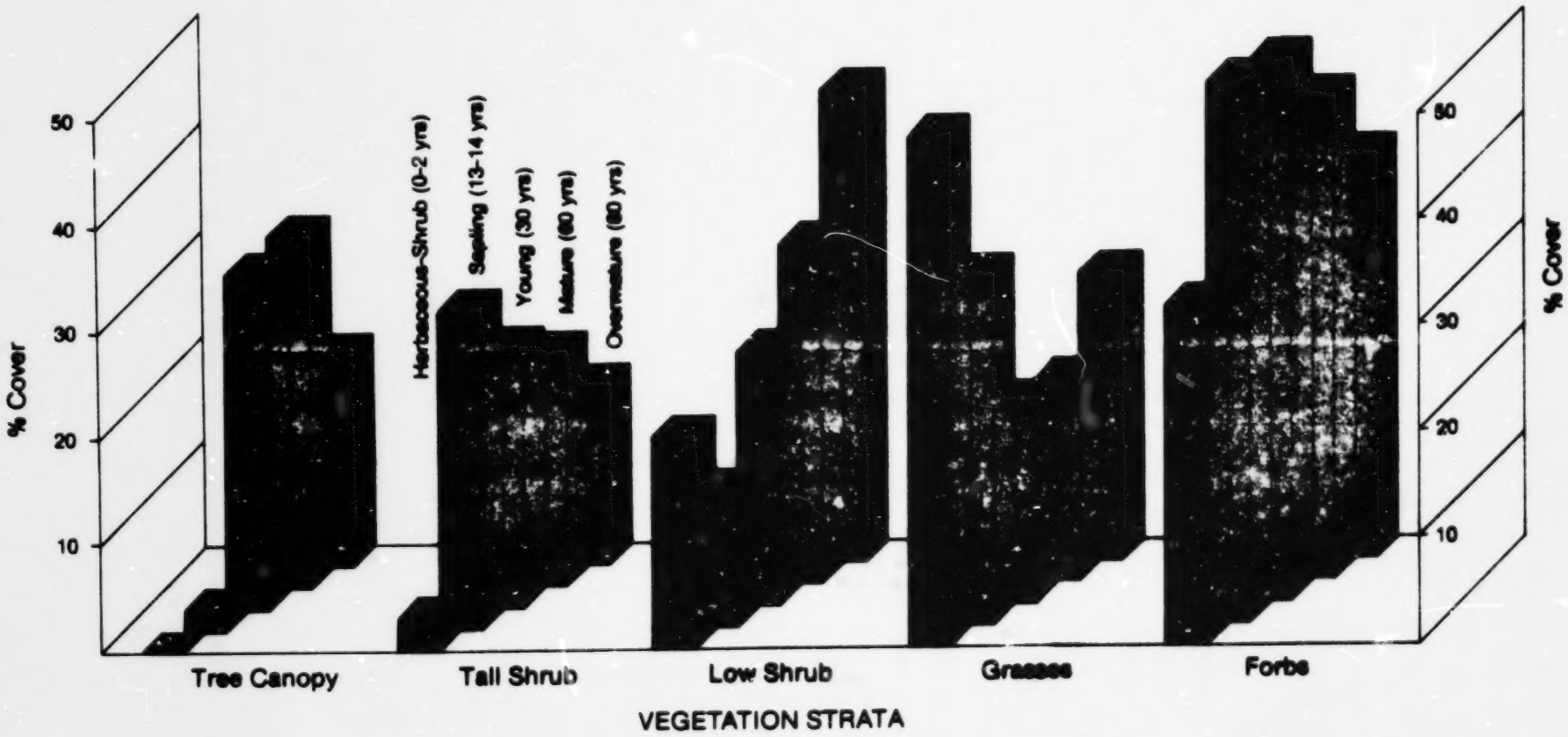


Figure 9. Changes in forest structure related to succession of aspen forests.

changes in the composition of the herb layer with grass cover decreasing and forbs showing a corresponding increase.

By age 30, pronounced changes in habitat structure are evident. Young or maturing seral stands exhibit a relatively dense canopy cover. Cover values for tall shrubs and grasses show a decrease while low shrubs start to increase in abundance. These trends continue as a stand proceeds to maturity. Canopy cover values are only slightly higher at age 60 than age 30, however the height, thickness and volume of the canopy are substantially increased. Mature stands are also characterized by low cover values for grasses, high cover values for forbs and an increasing cover of low shrubs. Changes in vegetation composition also occur in older stands. White spruce normally begins appearing in the shrub layer after age 30. White spruce was prominent in the tall shrub and intermediate tree layer of the 60-year-old stands. In the absence of any major disturbance, boreal aspen stands in Alberta will ultimately proceed to a climatic climax white spruce forest. However, factors including seed availability and site potential have a pronounced influence on the rate at which white spruce will replace aspen.

By age 80, mortality of trees becomes pronounced. Canopy cover decreases and the resulting increase in light penetration causes an increase in the cover of low shrubs and grasses. Decay and stem breakage become pronounced, causing a dramatic increase in the abundance of large diameter snags and deadfall.

Bella and DeFranceschi (1980) report that the culmination of mean annual increment (MAI) occurs at around 30 years for fully stocked aspen stands in western Canada. This period would be somewhat longer on poor sites and shorter on good sites. MAI also appears to culminate 1 or 2 years earlier in Saskatchewan than in Alberta (Bella and DeFranceschi 1980). Management for maximum biomass production would therefore involve a rotation age of around 30 years. In terms of the implications of short-rotation management for wildlife, it is obvious that the normal successional process will be truncated, resulting in a greater incidence of young, even-aged forest stands and a reduction in the amount of mature and old growth forest. Therefore, wildlife species that depend on habitat components present only in mature or over-mature aspen forests would be negatively affected, while species that occupy

niches present in younger forests will benefit. In the following sections, the probable impacts of this management strategy on each of the principal faunal groups are discussed.

4.1.2 Birds

As we have shown in this report, both the floristic composition and structure of aspen forests undergo pronounced changes as a forest ages. There is a corresponding change in the number and type of niches available for wildlife. Consequently, bird communities go through a process of successional replacement in which species adapted to early successional stages are replaced by other species as a forest ages. To achieve maximum species diversity a forest stand has to go through its entire life cycle. Under short-rotation management programs, the normal successional process would be repeatedly interrupted before stands have undergone one-half of their natural life cycle. A major objective of this study was to quantitatively determine how short-rotation management would effect the species composition and density of birds inhabiting aspen forests.

The results of our studies indicate that the density of breeding birds declines as the forest ages. On the Medicine Lake plots, the combined density declined from 656 territories per 100 ha at age 14 to 312 territories at age 30 and 231 territories at age 80 (Figure 10). Use of clearcuts is relatively low during the first two years, with an observed density of 110 territories per 100 ha. The high densities observed in the 14-year-old stands largely reflects the presence of a few species such as the least flycatcher, yellow warbler and American redstart that reached high densities in the younger stands. In terms of overall density therefore, the numbers of breeding birds using forests managed for a short rotation are expected to increase.

While aspen stands at the sapling stage support the highest density of breeding birds, they appear to be less important as habitat for winter residents. Winter bird population densities determined on three study grids in 1980-81 varied from 58 birds/100 ha at age 14 to 125 birds/100 ha at age 30 and 100 birds/100 ha at age 60 (Table 10). Some of the bird use in the 14-year-old stand was related to the presence of remnant snags, which would not be present in managed stands.

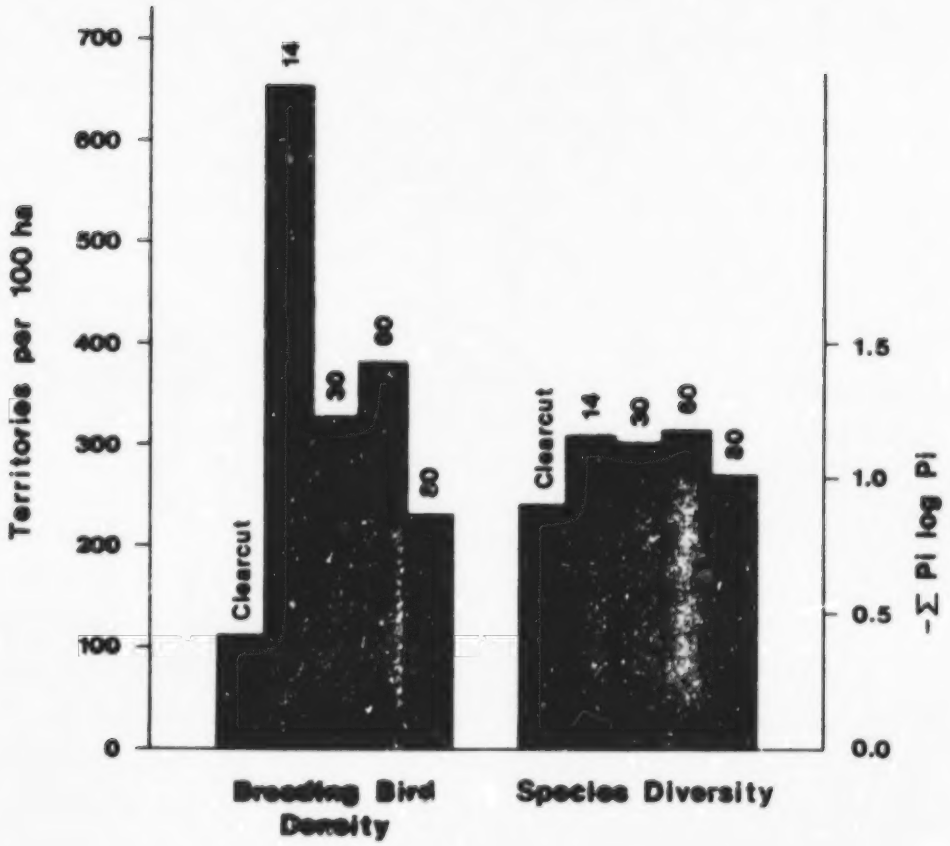


Figure 18. Density and species diversity of breeding birds by forest age class in the Medicine Lake study area, 1981-82.

When woodpeckers are eliminated, the winter bird density in the 14-year-old stand is reduced to 46 birds/100 ha. It appears therefore that winter bird densities may decrease somewhat under short-rotation management.

The diversity of avian species inhabiting aspen forests also changes as the forest matures, however the changes are less dramatic. Species richness (number of species) increased from 10 species in recent clearcuts to 25 species in 14-year-old stands before decreasing to 22 species in 30-year-old stands, 21 species in 60-year-old stands and 14 species in 80-year-old stands. In terms of the commonly used diversity index, which reflects both species richness and each species evenness in numbers within the community, it appears that overall species diversity changes very little from age 14 to age 80 (Figure 10). This is in contrast to the findings of many other workers (working in other forest types) who have reported that avian species diversity increases as succession procedes toward climax vegetation (Johnson and Odum 1956, Shugart and James 1973).

The large number of species and complex habitat relationships creates a conceptual problem when attempting to evaluate and describe the impact of an activity such as timber harvesting on avian communities. According to the classical definition, each species occupies a unique position in a community which is referred to as a niche. In practice, it has proven difficult to define the functional characteristics of a niche and an extensive literature has developed concerning niche and competition theory. Hutchinson (1958) defined a niche as a multi-dimentional hypervolume in which physical habitat structure may comprise one dimension. In reviewing resource partitioning Schoener (1974) concluded that in the case of birds, habitat dimensions were more important than food-type dimensions or temporal dimensions. Other authors have concurred that habitat structure is the principal factor influencing avian habitat use (Anderson 1979, MacArthur and MacArthur 1961, DesGranges 1980, Willson 1974).

A number of approaches have been developed for grouping bird species on the basis of their relationship to their habitat. A popular concept among many avian ecologists has been the partitioning of avian communities into groupings called guilds. A guild can be defined as "a group of species that exploit the same class of environmental resources in a similar way" (Root 1967, cited in Samson 1979). In practice, guilds have most often been defined in terms of similarities in

location or method of foraging or in terms of similarities in nest site selection using morphological, behavioral or ecological data (Flack 1976, Holmes et al. 1979, DesGranges 1980, Willson 1974). The life form approach is a similar concept developed by biologists involved in forest wildlife management in the Blue Mountains of Oregon and Washington (Thomas 1979). "Life forms are groups of wildlife species that exhibit similar habitat requirements for both feeding and reproduction" (Thomas 1979). Like the guild concept, the life form approach is a useful means of grouping species with similar habitat requirements that should respond in similar ways to habitat alteration. These approaches also have certain disadvantages however. The biologist is required to make subjective decisions concerning the classification of structural communities and species utilization of a structural community for feeding and reproduction (Niemi and Pfannmuller 1979). Another difficulty with this approach is that it requires biological information on the functional relationships within a faunal community that often does not exist. During recent years, biologists have begun to employ various multivariate statistical approaches in avian community analysis (Niemi and Pfannmuller 1979, Holmes et al. 1979, Rice 1978). Multivariate procedures provide a means of objectively determining bird species-habitat relationships on the basis of measureable characteristics of the community. It enables a large number of correlated variables to be analyzed simultaneously to isolate those factors responsible for similarities or differences between species.

In the present study we employed cluster analysis and principal components analysis to determine bird species habitat relationships in the Medicine Lake area. These analyses provided us with two important tools required to predict avian community responses to timber harvesting. It enabled us to identify species associations, that is groups of species which exhibit similar affiliations with respect to particular habitat variables or successional stages. Secondly, it enabled us to identify the key habitat components associated with each group of bird species. Although this approach tends to be mathematically complex in comparison to the more subjective methods of guild or life form analysis described above, we consider it a more straightforward approach in that it enabled us to objectively combine a large number of species into conceptually manageable groupings and at the same time identify key habitat components without the need to first unravel the complex functional interrelationships between bird species and the components of their habitat.

The results of these analyses showed that bird species use of aspen forests was primarily influenced by structural habitat features related to successional stage or stand age. Principal component analysis indicated that bird use was most strongly influenced by the development of the deciduous canopy (height, cover, thickness, volume). This component alone accounted for 57% of the variation explained by the analysis. Other important variables were the extent of coniferous cover and the amount of tall and low shrub cover.

As an aspen forest ages therefore, the structural components that affect bird use also change. Although species diversity remains relatively constant, the species composition of the avian community changes as the stand matures. The successional replacement of birds can be illustrated by comparing the relative density of each bird species between forests of different ages (Figure 11). Although most species occurred in more than one age class, most showed a preference for stands that were either younger or older than 30 years.

As we described earlier in the report, species in Bird Association 1 occurred in habitats characterized by a well-developed deciduous canopy and an increasing amount of conifer cover. These features are representative of older forest stands. Most of the species in this association occurred in the highest densities in the 60-year-old stands. These species would be adversely affected by short-rotation management. Although most would continue to be represented in younger stands, they would be present in greatly reduced numbers. The western tanager occurred only in the 60-year-old stands. Swainson's thrushes, tanagers and chipping sparrows nest in conifers and may not find suitable nesting habitat in the younger managed stands. The abundance of juncos in the 13 to 14-year-old stand may have been related to the abundance of deadfall which provided suitable nesting sites. Consequently, this species may become less abundant in managed stands. Red-eyed vireos benefitted from remnant clumps of mature aspen in the 14-year-old stand, therefore this species may also decrease in abundance in managed stands. Several species in this group however, including the black capped chickadee, Tennessee warbler, mourning warbler and white-throated sparrow, are capable of feeding and nesting in aspen stands of various ages and would therefore be less affected by short-rotation management.

Members of Bird Association 2 were primarily associated with the tall shrub-sapling successional stage. Species, including the flycatchers, warbling vireo,

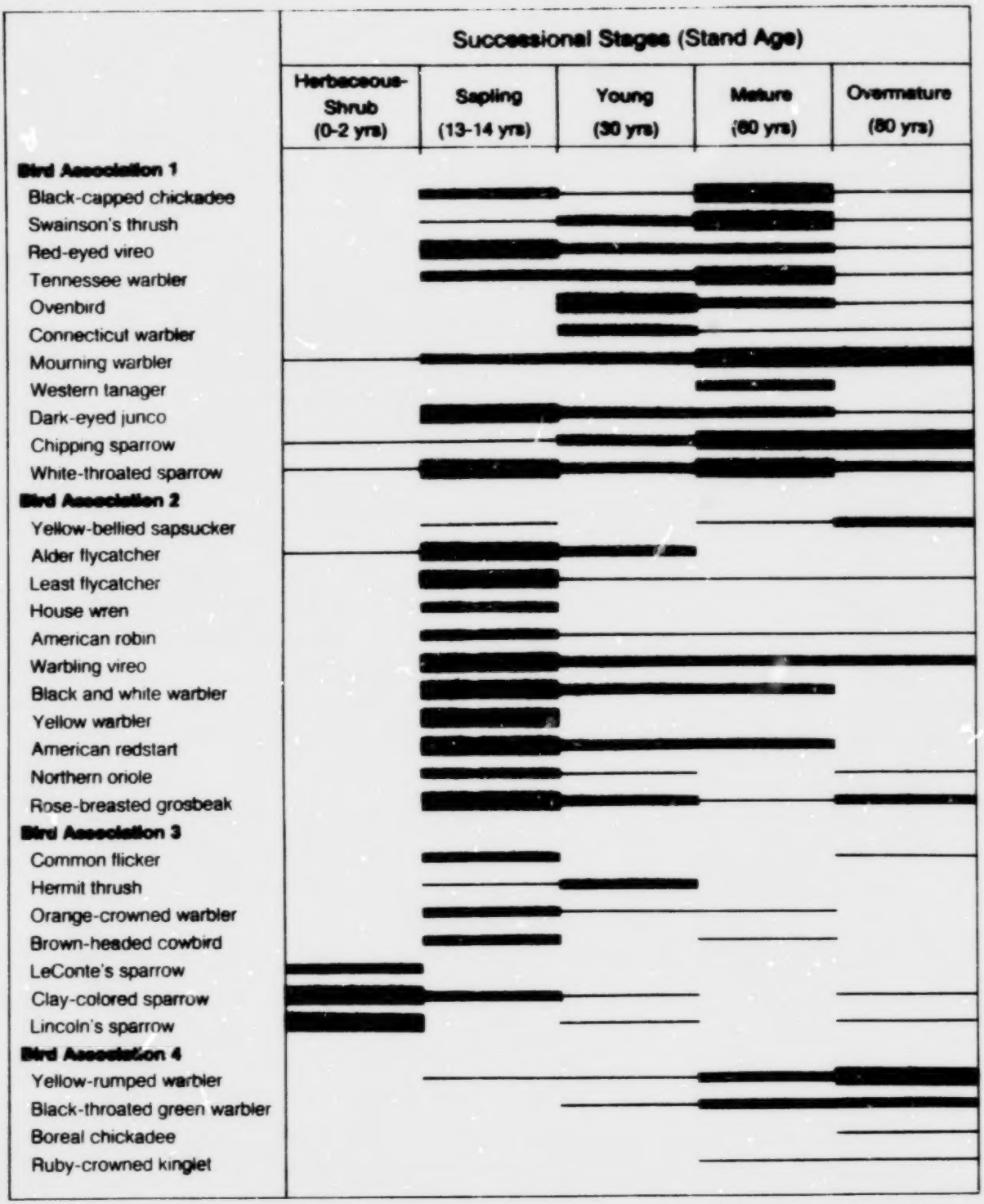


Figure 11. Successional replacement of birds in aspen forests. Line thickness indicates relative abundance.

warblers and rose-breasted grosbeak, which are typically associated with the tall shrub layer, would benefit from short-rotation management. The northern oriole, however were present only in areas supporting remnant veteran trees and therefore would likely not benefit from short-rotation management.

Species in Bird Association 3 were associated with open habitats, characterized by a well-developed, low shrub layer and low amounts of deciduous or coniferous canopy cover. These species occurred in greatest numbers in the recently clearcut areas or in the 14-year-old stands where occassional grassy clearings resulting from poor regeneration resulted in habitat features similar to those found in the clearcut habitats. The LeConte's, clay-colored, and Lincoln's sparrows, which feed on the ground in open areas, and the orange-crowned warbler, which exhibited a preference for an open, tall shrub layer, would benefit from short-rotation management. Flickers may have been attracted by the abundant supply of carpenter ants in the snags and deadfall present in the 14-year-old stand and consequently may not benefit from short-rotation management since these habitat elements would become less abundant. We are unable to explain the presence of the hermit thrush in this habitat since this species is more typically associated with mature mixedwood or coniferous forests.

Bird Association 4 was associated with habitats characterized by a well-developed conifer and deciduous canopy cover and a high amount of conifer cover in the tall shrub layer. These species, like those in Bird Association 1 are clearly associated with older stands, where white spruce, the climax tree species, are beginning to replace aspen. The yellow-rumped and black-throated green warblers, the boreal chickadee and the ruby-crowned kinglet all rely on the presence of conifers for nesting habitat. These species are therefore expected to disappear or occur in greatly reduced numbers in areas managed under short rotation.

A group of birds that would be strongly affected by short-rotation management is a unique association comprised of snag-dependent birds. As we discussed earlier in the report, the abundance of snags would be greatly reduced in aspen forests under short-rotation management, since the rotation period would greatly reduce the amount of natural mortality in the stand and snags that would form would be too small to be of value to the majority of the cavity nesting species.

Flack (1976) demonstrated that use of aspen forests by woodpeckers depended on the availability of snags with a dbh of at least 15 cm. Since it normally takes aspen 30 to 40 years to grow to this size (Maini and Cayford 1968), stands managed under short-rotation will generally be devoid of suitable nesting sites for woodpeckers. During the present study, a pronounced increase in habitat use by cavity excavators and cavity-dependent birds occurred with an increase in stand age from 60 years to 80 years. Species that would be affected by short-rotation harvesting include cavity excavators such as the pileated woodpecker, hairy woodpecker, common flicker, yellow-bellied sapsucker and black-capped chickadee, and cavity-dependent species such as the red-breasted nuthatch, house wren and tree swallow. While yellow-bellied sapsuckers sometimes nest in snags, they prefer to nest in live trees and would be less severely affected by the loss of snags per se. However, this species is also vulnerable to short-rotation harvesting since it apparently shows a strong preference for mature aspen (20-25 cm dbh) infected with heartrot (**Fomes igniarus**) (Kilham 1971).

Several species of birds that were present in the study area were not included in the analysis of bird associations. These included birds that were not territorial on the study plots, species with large territories that were rarely recorded and species that were present in densities too low to provide a sufficient sample of observations. One of these was the ruffed grouse, which is the most important game bird species in aspen forests of western Canada. Ruffed grouse were recorded on both 14-year-old grids and two of the three 30-year-old grids in 1982, however since this species was in the low phase of its population cycle, densities were very low. Other authors have reported that ruffed grouse use aspen stands of various ages during different parts of their life cycle. Young aspen stands of 1 to 10 years provide important brood rearing habitat because these areas provide insect food for chicks, open ground for easy travel and protection from avian predators (Euler 1979). As the chicks mature their diet switches from insects to aspen leaves, berries and fruit of woody and herbaceous plants, which are more abundant in stands of 10 to 30 years of age. These sapling and pole-sized stands also provide breeding and overwintering cover (Perala 1977, Ohmann et al. 1978). Stands older than 25 or 30 years are considered important for nesting and feeding areas. The staminate (male) flower buds of aspen are the most important food source in winter and spring. Even drumming logs and nest sites are located near clones of male aspen (Gullion 1972). Ruffed grouse are therefore dependent on a diversity of successional

stages. Gullion and Svoboda (1972) recommended clearcutting aspen in small (10 ac) units on a 40 to 50-year rotation to achieve habitat objectives for ruffed grouse. Harvesting on a 30-year rotation would increase the amount of habitat avilable for breeding and brood rearing but would decrease the availability of older stands required for nesting and winter and spring feeding. Because of their dependence on a number of successional stages, the amount and arrangement of stands of various ages is also important. Maintenance of even-aged stands over large (greater than 10 ha) areas would likely result in a reduction in numbers of ruffed grouse.

In summary then, most of the 60 or more bird species that commonly inhabit aspen forests would be affected in some way by short-rotation harvesting. Species adapted to early successional stages or forest edges would benefit while those species that occupy niches found only in older forests would be adversely affected. Approximately equal numbers of species would be positively and negatively affected. Of the 60 species recorded in the Medicine Lake area, 20 (33.3%) would be expected to show increases in numbers under short-rotation management, 21 (35.0%) would decrease in abundance, while 19 (31.7%) would not be strongly affected one way or the other. In many cases the actual effects would depend on the nature of the harvesting program; that is, the size and shape of cutblocks, the interspersion and juxtaposition of forest stands of different ages, and the amount of uncut residual forest. For example, species such as the goshawk, common flicker, ruby-crowned kinglet, yellow-rumped warbler, black-throated green warbler, western tanager, evening grosbeak and pine siskin are able to use young stands or ecotones for feeding but require older forests for nesting. The impact on these species would depend on the amount of mature forest retained for nesting habitat and its spacial relationship to younger forest stands.

4.1.3 Ungulates

The suitability of managed forests as habitat for ungulates depends on the degree to which they satisfy the basic needs of each ungulate species for food, cover and space. Timber harvesting affects ungulates by altering the quantity, quality and juxtaposition (arrangement of food and cover in time and space) of these elements.

Moose, elk, mule deer and white-tailed deer all inhabit boreal aspen stands in western Alberta. Although these species vary in the relative degree to which they feed on browse or herbaceous forage during the snow-free period, all are considered primarily browsers during winter. They would therefore benefit from the increased browse production that would result from the conversion of mature or old-growth forest to younger successional stages.

The results of this study show that browse availability in aspen forests decreases dramatically as a forest ages (Figure 12). The annual biomass yield of browse decreased from 210.4 kg/ha at age 14 to 40.4 kg/ha at age 30 and 19.9 kg/ha at age 60. Browse production is more than 10 times greater in regenerating stands than it is in mature stands. These differences may be even more pronounced since maximum browse production might occur prior to 14 years. Wolff and Zasada (1979) reported that browse production in aspen stands in Alaska was highest during the first five years. A rapid response to clearcutting in the Medicine Lake area was also apparent with browse yield more than doubling to 102.7 kg/ha after one growing season.

As we noted elsewhere in the report, we have assumed that the changes in habitat suitability that will occur after clearcutting are similar to the changes observed between successional stages in stands of fire origin. We are not certain however to what extent browse production estimates for fire successional stands are representative of clearcut stands of the same age. In the case of aspen, the mechanism of regeneration is the same for both fire and clearcutting. Aspen most commonly reproduces by suckers, which arise from the lateral roots of parent trees. Suckering is triggered by burning, cutting or windthrow of the parent stand (Perala 1977) which creates relief from apical dominance effects (Maini 1972). It is further stimulated by insolation-induced increases in soil temperature resulting from disturbance of the litter layer (Maini 1968, Steneker 1976). Factors such as the method and timing of clearcutting are reported to influence the intensity of suckering, however. The best results are apparently obtained when methods and equipment are employed that minimize damage to the parent root system. Perala (1977) reported that "shearing on frozen soils (with a sharp blade) will least disturb the parent root system and maximize sucker production". Other workers have also observed that maximum sucker production occurs when cutting takes place during the dormant period

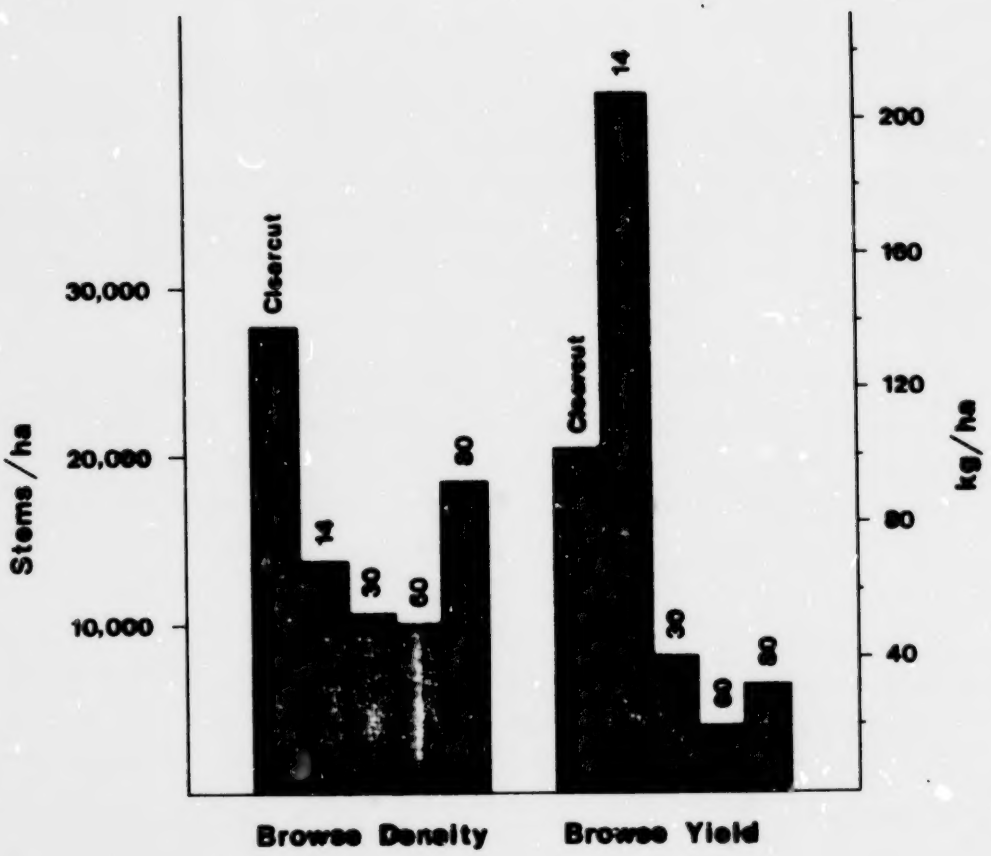


Figure 12. Production of principal ungulate browse species by forest age class in the Medicine Hat study area, 1982.

(Stoeckeler and Macon 1956, Steneker 1976, Bailey pers. comm.). Stoeckeler and Macon (1956) found that late summer cutting produced only 74-78% of the number of suckers produced by dormant season cuts. Bella and DeFranceschi (1972) however report that 50% more suckers can be expected during the first five years when aspen stands are cut during summer.

Forage production was also lower in the older stands, with the total dry weight biomass of forbs and grasses declining by 43% from age 30 (1152.5 kg/ha) to age 60 (652.1 kg/ha) (Table 8). Production of grasses was highest in the 13-year-old stand while production of forbs was highest in the 30-year-old stand. Leaf biomass available to ungulates was also highest in the 13-year-old stand (51.2 kg/ha).

Short-rotation management would therefore greatly increase the amount of summer forage and winter browse available to ungulates. The higher browse and forage production in younger stands was reflected in observed patterns of habitat use by ungulates at Medicine Lake. Pellet group densities for moose were highest in the 13-year-old stands, while the highest densities for elk and deer were in the 1-year-old clearcuts. Hunt (1976) reported similar results in a study of the effects on ungulates of clearcutting in aspen forests in east-central Saskatchewan. He reported that winter densities of moose and elk were 56% and 148% higher on cutovers than in uncut areas and that elk preferred younger (less than 5 years old) clearcuts while moose preferred older (9-10 years old) clearcuts.

While there is general agreement that clearcutting mature forest increases the amount of available browse and forage, the benefits to ungulates that might be realized depends on the extent to which their cover requirements are also provided for. A number of authors have noted that ungulate utilization of cutovers is governed to a large degree by the size and shape of the cutblocks and the amount of remaining uncut forest available for cover (Tomm et al. 1978, Hunt 1976). The requirements for cover differ between the various ungulate species.

All of the ungulate species require hiding cover which provides them with a sense of security or protection from harassment. This requirement affects their willingness to use clearcuts and, in the absence of an adequate amount of

effective hiding cover, large clearcuts may not be used even though they offer an attactive food supply. Lyon and Jenson (1980) reported that the willingness of deer and elk to use clearcuts in Montana was locally modified by past experiences. Consequently, these species showed a greater willingness to use large clearcuts in areas where large natural openings were present. They felt that the presence of roads was an important factor affecting elk use of clearcuts. Tomm et al. (1981) also found that harassment was a major factor affecting use of clearcuts by moose in west-central Alberta.

Local differences in environmental factors such as landscape patterns (presence of natural openings) and harassment perhaps accounts for the large range in size of clearcuts reportedly favored by ungulates in the literature. For moose, Oldemeyer and Regelin (1980) concluded that cutblocks in Alaska should not be less than 3 sq km in size. Telfer (1974) reported that moose will use 1.3 sq km cutblocks. Peek et al. (1976) recommended that cutblocks be at least 20 ac (8.1 ha) in size for moose. Parker and Morton (1978) reported that in Newfoundland, moose made maximum use of cut blucks that were 40-50 ha in size. Tomm et al. (1981) found that moose in west-central Alberta favored clearcuts 16.6-32.4 ha in area while Stelfox (1981) recommended a maximum clearcut size of 40 ha for an area in west-central Alberta containing a mixed population of moose, elk and deer. Lyon and Jenson (1980) concluded that the optimum size of clearcut for deer in Montana is 24 ha and found that elk preferred smaller clearcuts because they had a higher security requirement than deer. Drolet (1978) reported that white-tailed deer in eastern Canada tolerated clearcuts up to 60 ha in size. However, McCaffery and Creed (1969) reported that the use of forest openings by white-tailed deer in Wisconsin declined as the size of the clearing increased above 0.8 ha.

Since distance from cover appears to be the major factor affecting the willingness of ungulates to use large clearcuts, the width of cutblocks may be more important than the total area. Oldemeyer and Regelin (1980) reported that moose in Alaska randomly used clearcuts to a distance of 300 m. Hamilton and Drysdale (1975) reported that use patterns by moose were not restricted by cutovers less than 200 m wide. McLennan (1975) found that random distribution by moose occurred to a distance of 114 m from cover in aspen clearcuts in Saskatchewan. Tomm et al. (1981) concluded that cutblocks 320-400 m wide

were acceptable for moose in areas of low harassment while widths of 120-160 m were preferred in areas of high harassment. Wallmo (1969) compared use of clearcut strips that were 20, 40, 60 and 121 m wide by mule deer in Colorado. Strips that were 60 m wide received the most use while the 20 m and 121 m wide strips received the least use.

It appears probable therefore that the potential benefits of short-rotation harvesting to ungulates in terms of increased food production would diminish if the management plan involved the use of clearcuts greater than about 400 m in width. The central portions of larger clearcuts may not be used until the regenerating aspen and shrub cover is high enough to provide effective hiding cover. In aspen forests it could take 10 years or longer for effective cover to develop. Hunt (1976) reported that the retention of residual cover blocks enables moose to make use of the central portion of large clearcuts.

In addition to hiding cover, some ungulate species have an additional requirement for thermal cover. The aspen regions of western Canada are characterized by long, cold winters. During winter, the quantity and quality of available food declines and snow may severely restrict ungulate movements and feeding activity. As a result, winter is a period of thermal stress for ungulates. During severe winters or during intervals of severe weather conditions, ungulates often move into favorable habitat areas which offer warmer microclimates, reduced snow depths or greater browse availability.

The availability of thermal cover has been shown to be an essential habitat element for white-tailed deer in the parkland and boreal mixedwood regions of Alberta (Westworth 1979, Westworth and Brusnyk 1983). This requirement appears to be primarily related to snow depth. A number of workers have reported that snow depths greater than 40 cm severely restrict the movements of white-tailed deer (Kelsall and Prescott 1971, Drolet 1976, Telfer 1970). Westworth (1979) reported that during a severe winter in northeastern Alberta, when the average snow depth in deciduous habitats reached 58 cm, bedding activity of white-tailed deer was confined to sites containing white spruce cover and feeding trails seldom extended more than 50 m from coniferous cover. Similar findings were reported by Westworth and Brusnyk (1983) in a detailed study of winter habitat use by white-tailed deer along the northwestern limit of

the aspen parkland region in central Alberta. They found that during early winter deer were dispersed throughout deciduous habitats but in late winter when the average snow depth reached 51 cm, they confined their feeding and bedding activity to sites containing some coniferous cover. Although white spruce comprised less than 2% of the forest cover in this region it accounted for 74% of the bedding sites. At these sites the overhead cover provided by white spruce averaged 86%. Deer also exhibited a selection for large trees at bedding sites (mean dbh = 30.8 cm) and a strong orientation with regard to direction from windbreaking cover.

A number of other authors have also noted the importance of coniferous cover for winter survival of white-tailed deer (Verme 1968, Ozoga 1968, Drolet 1976, Euler and Thurston 1980). Conifer stands offer a warmer microclimate for deer because windflow and windchill factors are lower (Ozoga 1968) and the dense canopy reduces radiant heat loss (Moen 1968). Westworth and Brusnyk (1983) concluded that, because browse availability is usually much lower in coniferous stands than in more open deciduous stands, optimum winter habitat for white-tailed deer contains small stands of conifers interspersed throughout areas containing a high density of preferred browse species.

In eastern North America, coniferous cover has been shown to be important for moose as well during winter (DesMeules 1965, Telfer 1970, Peek et al. 1976). Telfer (1970) reported that in New Brunswick moose showed a preference for open or deciduous cover types in mid-winter when snow depths were 32-48 cm but used dense coniferous and mixed stands significantly more than would have been expected in late winter when snow depths in open cover types ranged from 93 to 112 cm. Studies of winter habitat selection by moose in Alberta have not shown a need for coniferous cover however. This appears to reflect the lower snow depths experienced in the west and the cold, dry winter climate which usually results in soft, uncrusted snow conditions. For example, the mean snow depth at Rocky Mountain House from 1955-80 was aproximately 30 cm during the deepest month (Figure 7). Some observers have reported that snow depths of less than 70 cm allow unimpeded travel by moose (Kelsall and Prescott 1971, DeMeules 1964). Elk are also expected to be more tolerant of deep snow than deer, however information is lacking on their winter cover requirements in boreal aspen forests.

In summary then, it appears that the effects of short-rotation management on ungulates will be beneficial as long as management programs include silvicultural options that will meet the various species needs for cover. Moose will greatly benefit from the increased browse production that will occur during the first 15 years of the rotation. Studies in southwestern Alberta have shown that browse availability is the principal factor affecting moose distribution (Telfer 1978, Westworth et al 1984). Telfer (1978) concluded that the carrying capacity for moose is closely related to the available standing crop biomass of browse. One can obtain a crude estimate of the mean annual browse yield under short (30 year) and long (80 year) rotations by assuming that the estimates of browse yield obtained for 1, 14, 30, 60 and 80-year-old stands represent yields for each year of the period encompassed by the midpoints between these intervals. Calculated in this way the mean annual browse yield would increase by approximately 100% from 70.2 kg/ha in an 80-year rotation to 139.9 kg/ha in a 30-year rotation. This would suggest that the average carrying capacity for moose would approximately double under short-rotation management.

Elk and deer would also benefit from the increased browse and forage production, however potential benefits would depend on the size and shape of clearcuts and the temporal and spatial arrangement of cutovers. Stands at least 10 to 15 years old adjacent to new clearcuts are required to meet the requirements of all four ungulate species for hiding cover. As well, white-tailed deer and perhaps elk have an additional requirement for thermal cover. During severe winters, white-tailed deer are dependent on coniferous overhead cover that is only available in stands that are at least 50-60 years old. Thermal cover requirements would therefore only be met by allowing some stands to mature into old growth forest.

4.1.4 Snowshoe Hare

Snowshoe hares were included among the groups of wildlife receiving detailed investigation during this study. This reflects the role of the snowshoe hare as a major herbivore in boreal forest communities. During high phases of its 10-year population cycle, it may consume as much or more of the available browse supplies as larger herbivores such as moose, and it is capable of influencing forest stand development by causing mortality or slowing growth of woody plant species (Oldemeyer 1983). Snowshoe hares also play an important part in

population regulation of several important predator species. Changes in the population cycle of hares have been shown to cause fluctuations in numbers of lynx (van Zyll de Jong 1977, Keith 1974, Brand and Keith 1979), coyote (Nellis and Keith 1976, Keith et al. 1977) and great-horned owl (Adamcik et al. 1978).

The present study began during the high phase of the population cycle and extended through the first year of the population decline. Pellet densities declined by approximately 50% from 1981 to 1982 (Table 28). During both years there was a pronounced difference in hare use between the different successional stages. Significantly higher use was recorded in the 14-year-old stands and use generally declined with forest age. No use was observed in the 2-year-old clearcut. Similar findings are reported by Poll (1981) who found levels of hare use in an 18-year-old aspen stand to be approximately four times higher than in mature, unburned stands.

As discussed earlier in the report, the high use recorded in the 14-year-old stands apparently reflects the cover value provided by the well-developed, tall shrub layer and the high density of deadfall. The presence of cover appeared to be more important to habitat use by hares than browse availability, since availability of preferred browse species such as rose and raspberry increased in the older stands. On the clearcut plots the dense, regenerating shrub growth had not yet achieved sufficient height to provide protection from avian and mammalian predators. The older stands were characterized by a decreasing amount of tall-shrub cover (Figure 9), although some additional cover was provided by conifers which started becoming prominant in the 60-year-old stands. These results are in agreement with those of most other workers who have reported that cover provided by a dense, tall shrub layer is the principal factor affecting hare distribution (Van Camp and Telfer 1975, Conroy et al. 1979, Wolff 1980, Wolfe et al. 1982)..

Over the long-term, snowshoe hares might benefit from the replacement of aspen forests by climax coniferous forest stands. A number of authors have discribed the value of coniferous cover to hares (Van Camp and Telfer 1975, Conroy et al. 1979, Poll 1981, Wolfe et al. 1983). In addition to providing protection from predators, conifers offer thermal cover. Radiant heat loss is reduced under dense, coniferous canopies (Moen 1968) and microrelief provided

by snow shadows under conifers may reduce exposure to windflow and windchill. Several authors report significantly higher use of coniferous cover types in comparison to aspen (Poll 1981, Westworth and Brusnyk 1982, Wolfe et al. 1983). Using track count data, Poll (1981) recorded two times as much use of white spruce and unburned black spruce than was made of 18-year-old aspen in Riding Mountain National Park. In northeastern Alberta, Westworth and Brusnyk (1982) recorded snowshoe hare pellet densities (pellets/m^2) of 11.5 in white spruce, 11.2 in jack pine and 10.7 in black spruce as compared to 6.4 in aspen and 5.3 in balsam poplar habitat types. Some authors have also reported that aspen-conifer edges receive high use by hares (Poll 1981, Wolfe et al. 1982).

In assessing the potential effect of short-rotation harvesting of aspen on snowshoe hares, it therefore depends to some extent on whether one adopts a short-term or long-term prespective. It is probable that hares would benefit from eventual replacement of aspen by climax white spruce forest. This would not occur however in managed aspen stands. It is also apparent however, that this is not occurring naturally at a very fast rate. Periodic forest fires are maintaining large parts of the boreal mixedwood region in seral communities dominated by aspen or other fire successional species such as lodgepole pine or jack pine. On some sites overmature aspen may exist with little evidence of replacement by spruce.

In areas where aspen is being maintained as the dominant tree species, short-rotation management will be beneficial to hares. Short-rotation harvesting will increase the frequency and period of time in which aspen stands are in the productive, tall shrub-sapling stage. Decreases in the amount of deadfall in managed stands will result in lower cover values however, which could result in a somewhat lower carrying capacity than occurs in young stands of fire origin. Further benefits to hares would result from timber management strategies that attempt to maximize the diversity of forest types and successional stages and to maximize the amount of edge between new clearcuts and coniferous-dominated or shrubby stands that offer suitable cover.

4.1.5 Other Mammals

4.1.5.1 Small Mammals

Although small mammal populations were not investigated as part of the present study, the potential impacts of short-rotation management on this important group of mammals should be considered. Small mammals comprise a diverse faunal group that includes mice, voles, shrews and chipmunks. They are the most abundant group of mammals inhabiting aspen forests and are important as the basis of the food web for many species of carnivorous birds and mammals. Changes in the species composition and abundance of small mammal populations will alter habitat suitability for the predators that depend on them.

While small mammals have been extensively studied in other forest communities, comparatively little information is available on small mammal populations in boreal aspen forests. Westworth and Skinner (1980, 1981) and Westworth (1982) give results of a five year study of cricetid rodent populations in mature aspen-dominated mixedwood stands and recently clearcut areas in northeastern Alberta. Other studies have examined rodent populations in aspen parkland regions of Saskatchewan (Morris 1969) and Manitoba (Iverson and Turner (1973). These studies indicate that the most abundant species in aspen forests are the red-backed vole **(Clethrionomys gapperi)** and deer mouse **(Peromyscus maniculatus).** Other small mammal species may include the heather vole **(Phenacomys intermedius),** least chipmunk **(Eutamias minimus),** flying squirrel **(Glaucomys sabrinus),** masked shrew **(Sorex cinereus),** and pygmy shrew **(Microsorex hoyi).**

Red-backed voles are largely restricted to forested habitats (Clough 1964, Morris 1969, Grant 1970, Miller and Getz 1973, Crowell and Pimm (1976) although some authors have reported limited use of open grassland habitats in late fall and early winter (Iverson and Turner 1973, Westworth and Skinner 1979). Within forested habitats, factors that have been reported to influence their distribution include amount of debris cover (Gunderson 1959, Miller and Getz 1973) and available moisture (Bertsch 1954, Miller and Getz 1973). Deer mice however, are ecological generalists that occupy a wide range of habitat types. This species has been reported to successfully inhabit forests (Gashwiler 1959, Grant 1970, Petticrew and Sadleir 1974, Sullivan 1979), shrubby habitats (Rosenzweig and

Winakur 1969, Crowell and Pimm 1976) and grasslands (Wecker 1963, Hodgson 1972). Several authors have described the successful invasion of recently disturbed habitats, such as burns or clearcuts, by this species (Gashwiler 1959, Radvanyi 1963, Sims and Buckner 1973, Petticrew and Sadleir 1974, Hoover and Black 1976).

Westworth and Skinner (1979) reported that deer mice occurred in about equal densities in mature aspen stands and areas that had been clearcut three years previously. Red-backed voles however decreased in density from a maximum of 19.7 per ha on forested plots to a maximum of 1.6 per ha on cleared plots. The decreased number of red-backed voles was offset by a rapid invasion of meadow voles **(Microtus pennsylvanicus)** which reached densities of up to 83.3 per ha during the high part of the population cycle. Meadow voles are herbivores that feed primarily on the vegetative portions of graminoids (Zimmerman 1965, M'Closkey 1975, Grant 1971, Folinsbee et al. 1973) and some authors have reported that their density varies in relation to the density of grass cover (Eadie 1953, Hodgson 1972, LoBue and Darnell 1959, Birney et al. 1976).

On the basis of these studies it appears that short-rotation harvesting will alter the species composition of small mammal communities. Red-backed voles will disappear from clearcut areas and be replaced by non-forest species such as the meadow vole, which will occur as a temporary resident until the clearcut again assumes the characteristics of a forested habitat. However, since small mammal responses to aspen succession have not been reported, several unanswered questions remain concerning the period of time before the regenerating forest will be recolonized by red-backed voles, the period of time before the clearcut habitats become unsuitable for meadow voles, and the relative importance of young aspen stands in comparison to mature and old-growth forest stands.

Changes in the litter layer and the amount of deadfall could also adversely affect small mammals in managed stands. Deadfall provides cover, travel lanes and nest sites for several species of small mammals. It also provides a foraging area for species that feed on mosses, mushrooms, fungi and insects. The loss of large snags will reduce the availability of suitable nest sites and overwintering sites for flying squirrels, which sometimes occupy cavities created by woodpeckers.

It appears likely that the overall density of small mammals will increase, at least in the period immediately following clearcutting. This could result in increased densities of certain predator species. Westworth and Skinner (1979) reported intensive hunting of small mammals by marsh hawks on recently clearcut areas. Other avian predators, including short-eared owls **(Asio flammeus)** and hawk owls **(Surnia ulula)** also made greater use of the clearcuts and recently revegetated areas.

4.1.5.2 Beaver

Beaver were abundant along streams in the Medicine Lake study area and are common throughout the boreal mixedwood forest region where they rank as one of the most commercially important furbearers. The importance of aspen as food for beaver is widely known (Aldous 1938, Slough and Sadlier 1977, Gilbert 1979). Slough and Sadlier (1977) concluded that while other species such as willow and alder may be heavily used, aspen is generally required for beaver to reach high densities. They suggest that aspen forest is sufficiently important to allow management of beaver through its manipulation.

Removal of the forest cover by logging or forest fire may initially have a disruptive effect on beaver populations. Fuller (1953) documented a decline in beaver populations in the Northwest Territories during the 1940's following a number of large forest fires. Other authors however have noted that these disturbance factors play an important long-term role in beaver ecology by maintaining seral aspen stands (Lawrence 1964, Heiselman 1973, Kelsall et al. 1977).

By converting mature or overmature stands to young aspen stands and preventing succession to less desireable tree species, short-rotation management may be beneficial to beaver. Bella and DeFranceschi (1980) provide biomass yield data for the various components of aspen. Two of these components, stem bark and branches-leaves, represent fairly closely the components that are important as food for beaver (Figure 13). These data show that in the case of aspen stands growing on medium sites in Alberta, the maximum MAI occurs at age 29 for stem bark and at age 25 for branches and leaves. In forest management for wood production, the optimum rotation period is often based on the culmination of mean annual increment. This concept also has relevance to beaver management,

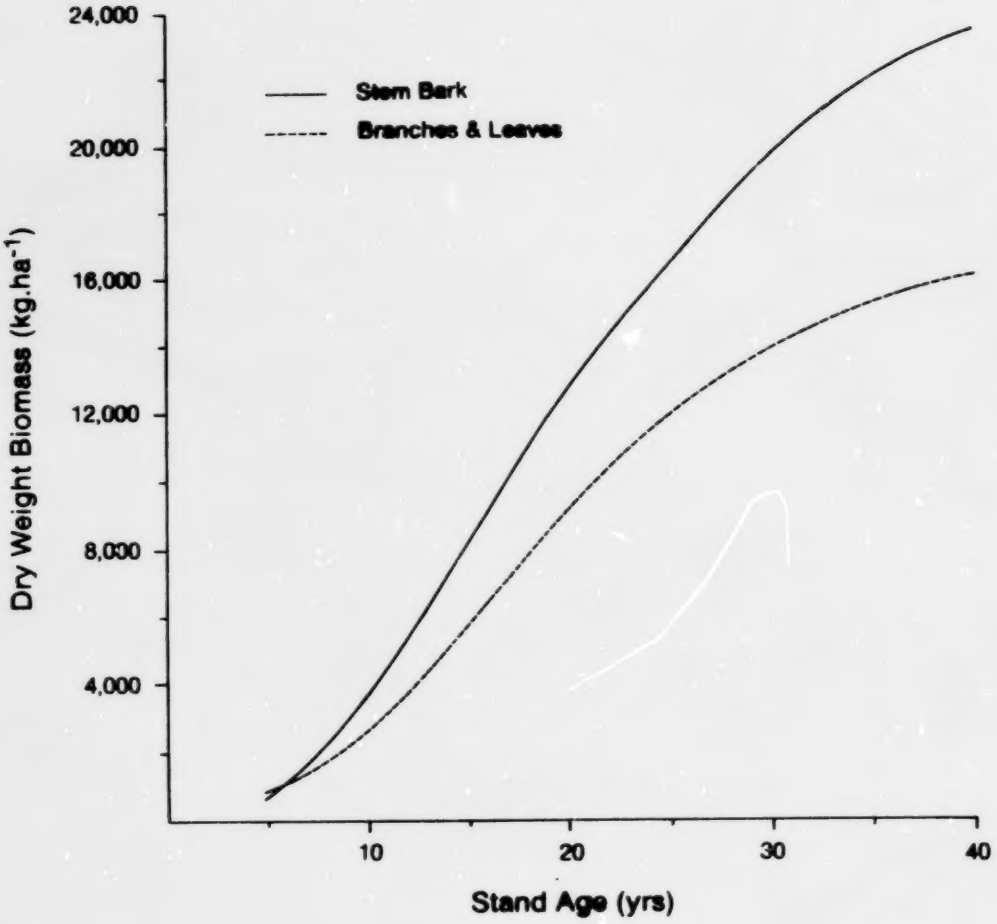


Figure 13. Biomass yield curves for two components of Alberta aspen stands (site index 20 m at age 50) (plotted from data provided by Bella and DeFranceschi 1980).

which suggests that short-rotation management has the potential of being an important habitat management technique. Again the actual effects of short-rotation management on beaver will depend on the size and crientation of cutblocks in relation to waterbodies and the sequence of harvesting operations. A preferred management option would involve closely spaced (200-400 m) cutblocks of varying ages to provide stability in food resources for beaver colonies.

4.1.5.3 Terrestrial Furbearers

Ecologically the terrestrial furbearers comprise a diverse group of mammals. They are also a poorly understood group. The lack of detailed, quantitative information of the habitat relationships of several species makes it difficult to accurately predict the effects of forest management practices.

Species that are usually considered to be the most sensitive to timber harvesting are those that inhabit mature or climax forest types. These include marten, which are affected by the loss of mature conifer forest (Dodds and Martell 1971, Soutiere 1979, Steventon 1979) and red squirrels, which are dependant on the availability of white spruce seed as food (Brink and Dean 1966, Rusch 1970, Wolff and Zasada 1975). Neither species is common in aspen forests, usually appearing only in late successional stages when white spruce becomes prominant. Over the long term, these species could be affected by a reduction in the amount of aspen succeeding to mixedwood or coniferous forest under short-rotation management programs.

Fisher are considered to be less of a 'climax' species than marten, apparently preferring mixedwood forests with interspersed stands of lowland conifers and tall shrubs (Todd 1978). This reflects their food habits. Fisher apparently rely heavily on snowshoe hares as a prey species (Quick 2953, Giesbrecht and Todd 1977) along with red squirrels, grouse (Quick 1953) and porcupines (Powell and Brander 1977, cited in Todd 1978). In northeastern Alberta, track counts showed that fisher preferred mixedwood (aspen-white spruce) habitats but used aspen stands in proportion to their availability (Westworth and Brusnyk 1982). It appears likely that fisher would be adversely affected by short-rotation management over extensive areas, although they could benefit from the increased prey abundance along the edges between clearcuts and mature (unmanaged) forest.

Black bears are capable of exploiting a wide range of habitats, however in the boreal mixedwood region of Alberta they apparently prefer mature deciduous and mixedwood forests (Young 1976, Fuller and Keith 1977, Ruff 1978, Westworth and Brusnyk 1982). In northeastern Alberta, Westworth and Brusnyk (1982) reported that the greatest proportion of summer feeding and denning activity occurred in mixedwood (white spruce-aspen) forest. Ruff (1978) reported a difference in habitat selection between age-sex cohorts of black bear populations in east-central Alberta, with adult males showing a preference for aspen while adult females and subadults selected mixedwood habitats. Mature white spruce-aspen or white spruce forests were selected to a greater degree than other available habitats for denning sites (Tietje and Ruff 1980).

Workers in other parts of North America have reported that black bears are often attracted to recently burned or clearcut areas because of increased food production, particularly berry-producing plants (Scotter 1964, Jonkel and Cowan 1971, Rogers 1976, Lindzey and Meslow 1977). Scotter (1964) reported that black bears were attracted to burned areas containing abundant berry crops in northern Saskatchewan. Rogers (1976) observed that black bears in Minnesota made higher use of logged areas than mature forest because of increased food production. He found that annual variations in insect and berry crops affected the productivity and survival of bears. In Washington, Lindzey and Meslow (1977) reported that black bears avoided the centers of recent clearcuts because of the lack of cover but preferred younger stands because berry-producing plants were 7-8 times more abundant than in older stands. They concluded however, that use of clearcuts was dependent on the size, shape and arrangement of cutblocks and the amount of edge between clearcuts and uncut forest.

Although black bear responses to logging have been extensively studied elsewhere, information is lacking on the effects of logging aspen forests. On the basis of the above studies, we suspect that, while bears would likely benefit from increased forage production on clearcuts, they would be adversely affected by the elimination of mature deciduous or mixedwood cover over large areas. Insects (eg. grubs, carpenter ants, wasps) appear to be a major summer food item for black bears in boreal aspen stands, consequently the loss of large diameter, decayed deadfall in managed stands would also be disadvantageous. Net benefits would probably occur under forest management strategies that maintained an

interspersion of old growth and managed stands and attempted to maximize the amount of forest edge.

Most of the other large carnivores are expected to benefit from short-rotation management. Wolves would benefit from the increased density of ungulate prey species, while lynx and coyotes would benefit from increased snowshoe hare abundance in young stands. Ozoga and Harger (1966) found that the interspersion of forest openings was important for coyotes in Michigan because they habitually hunted along edges or ecotone areas.

5.0 SUMMARY AND CONCLUSIONS

A study was initiated in west-central Alberta in 1981 to determine the potential effects of short-rotation harvesting of boreal aspen stands on major groups of wildlife. The study entailed a comparative evaluation of habitat conditions and wildlife use of aspen stands of different ages, including 1-, 2-year-old clearcuts and 14-, 30-, 60- and 80-year-old stands.

Results of the investigation showed pronounced differences in wildlife use among stands of different ages. These differences resulted from changes in habitat structure as aspen stands progressed from the herbaceous-shrub stage to mature and old growth successional stages. Many of these changes were related to development of the forest canopy. Canopy cover increased to a maximum at age 60 before declining in overmature stands due to mortality of trees. The most prominant structural characteristic of regenerating stands at the sapling stage (10-15 years) was the presence of a well-developed tall shrub layer. Tall shrub cover decreased as the stands matured while cover values for the low shrub layer tended to increase. Changes in the herbaceous layer closely followed the observed changes in canopy cover. Grass cover was highest on the 1-year-old clearcut and lowest in the 30- and 60-year-old stands. Grasses began increasing in abundance again in overmature stands as the canopy opened up. Conversely, forbs had the highest cover values in stands of medium age. Other important changes were the appearance of white spruce in the tall shrub and intermediate tree layers of the 60-year-old stands and the dramatic increase in abundance of large diameter snags and deadfall in the 80-year-old stand.

Avian communities also went through a process of successional replacement in which species adapted to early successional stages were replaced by other species as the forest matured. Multivariate analysis revealed that these changes were most strongly related to development (height, cover, thickness, volume) of the deciduous canopy. Other important variables were the amount of coniferous cover and the amount of cover provided by the tall and low shrub layers.

The impact of short-rotation harvesting on bird species will depend on whether or not they depend on habitat elements present only in stands older than 30 years. Species adapted to early successional stages or forest edges would be expected to benefit while those species that occupy niches present only in older

forests would be adversely affected. Approximately equal numbers of species would be positively and negatively affected. Of the 60 species recorded in the Medicine Lake area, 20 (33%) are expected to increase in numbers under short-rotation management, 21 (35%) would decrease in abundance, while 19 (32%) would not be strongly affected one way or the other. Among the species that would be adversely affected are the snag-dependent birds. The size of snags that would be produced under short-rotation harvesting would not provide suitable nesting sites for woodpeckers and most other cavity-nesting species.

The overall density of breeding birds is expected to increase under short-rotation management. In the Medicine Lake area the combined density of breeding birds was highest in the younger stands, declining from 656 territories/100 ha at age 14 to 312 territories/100 ha at age 30 and 231 territories/100 ha at age 80. Breeding birds made limited use of clearcuts during the first two years, with an observed density of 110 territories/100 ha. While young stands support the highest densities of breeding birds, winter residents preferred mature stands. Short-rotation management would therefore result in a reduction in the amount of suitable winter habitat.

Pronounced differences in habitat suitability for ungulates were also observed between different successional stages. Browse and forage production was significantly higher in the younger stands. The annual biomass yield of browse decreased from 210.4 kg/ha at age 14 to 40.4 kg/ha at age 30 and 19.9 kg/ha at age 60. Grass production was highest in the 14-year-old stand (400.6 kg/ha) while forbs were most abundant in the 30-year-old age class (889.6 kg/ha). Leaf biomass available to ungulates was also highest in the 14-year-old stand (51.2 kg/ha). The higher browse and forage production in younger stands was reflected in observed patterns of habitat use by ungulates. Pellet group densities for moose were highest in the 14-year-old stands, while the highest densities for elk and deer were in the 1-year-old clearcuts.

Short-rotation management would have a beneficial effect on ungulate populations, as long as management programs include silvicultural options that will meet the cover requirements of each species. Moose will greatly benefit from the increased browse production that would occur during the first 15 years of the rotation. Elk and deer would also benefit from the increased browse and

forage production, however potential benefits would depend on the size and shape of clearcuts and the temporal and spatial arrangement of cutovers. In addition to hiding cover, white-tailed deer have an additional requirement for coniferous overhead cover that is only available in stands older than 50 years.

Snowshoe hares similarly exhibited a preference for younger stands. Significantly higher use was recorded in the 14-year-old stands with use generally declining with forest age. No use was observed in the 1- or 2-year-old clearcuts. The preference shown by hares for the 14-year-old age class reflected the cover value provided by the well-developed tall shrub layer and the high density of remnant deadfall. Snowshoe hares would benefit from short-rotation management since the proportion of time that stands are in the productive, tall shrub-sapling stage would increase; however, lower cover values resulting from decreases in the amount of deadfall in managed stands could result in a lower carrying capacity than occurs in young stands of fire origin.

Changes in the abundance of most other species of mammals are also expected to occur under short-rotation management. Small mammal densities would likely increase, however species composition would change, with meadow voles and other species adapted to open habitats replacing forest species such as the red-backed vole on recently clearcut areas. Beaver would benefit from the increased food production in young aspen stands. Species such as marten, fisher and red squirrel, which inhabit mature or climax forest types, would be adversely affected by a reduction in the amount of aspen succeeding to mixedwood or coniferous forest under short-rotation management. Among the large carnivores, lynx and coyotes would benefit from increased snowshoe hare abundance in young stands and wolves are expected to benefit from the increased density of ungulate prey species.

The overall impact of short-rotation management of boreal aspen stands on wildlife will be highly dependent on the type of forest management plan adopted. Younger forest stands are more productive for many species, however potential benefits depend on the extent to which forest management plans include silvicultural options designed to satisfy each species requirements for food, cover and space. A number of species require habitat elements found only in mature or overmature forests, and consequently would be adversely affected.

These adverse effects would be mitigated by retaining residual, uncut stands, however this would involve trade-offs in wood biomass production. The maximum benefits and least adverse impact would occur under forest management programs designed both to meet the food and cover requirements of priority wildlife species and to maintain the species richness of the management area. Preparation of detailed, site-specific management plans by teams of experienced biologists and foresters or silviculturalists is an essential prerequisite for a responsible forest management program.

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APPENDIX I. Species list of trees and shrubs found in the Medicine Lake study area (nomenclature follows Moss 1959).

Common Name	Scientific Name
Aspen	**Populus tremuloides** Michx.
Balsam poplar	**Populus balsamifera** (L.)
White birch	**Betula papyrifera** (Marsh.
White spruce	**Picea glauca** (Moench) Voss
Lodgepole pine	**Pinus contorta** Laudon
Green alder	**Alnus crispa** (Ait.) Pursh.
River alder	**Alnus tenuifolia** Nutt.
Willow	**Salix** spp.
Low-bush cranberry	**Viburnum edule** (Michx.) Raf.
Saskatoon	**Amelanchier alnifolia** Nutt.
Red-osier dogwood	**Cornus stolonifera** Michx.
Buffaloberry	**Shepherdia canadensis** (L.) Nutt.
Bracted honeysuckle	**Lonicera involucrata** (Richards.) Banks
Twining honeysuckle	**Lonicera dioca** L.
Current	**Ribes** spp.
Wild red raspberry	**Rubus strigosus** Michx.

APPENDIX II. Common names, scientific names (after Moss 1959) and species codes of grasses, forbs and woody shrubs (less than 0.5 m in height) found in the Medicine Lake study area.

Common Name	Scientific Name	Code
Aspen	**Populus tremuloides** Michx.	ASPE
Balsam poplar	**Populus balsamifera** (L.)	BAPO
Blue fly honeysuckle	**Lonicera villosa** (Michx.) R. & S.	BFHO
Bracted honeysuckle	**Lonicera involucrata** (Richards.) Banks	BRHO
Currant	**Ribes** spp.	CURR
Green alder	**Alnus crispa** (Ait.) Pursh	GRAL
Low-bush cranberry	**Viburnum edule** (Michx.) Raf	LBCR
Red-osier dogwood	**Cornus stolonifera** Michx	RODO
Rose	**Rosa** sp.	PRRO
Saskatoon	**Amelanchier alnifolia** Nutt.	SASK
Snowberry	**Symphoricarpos albus** (L.) Blake	SNBE
White birch	**Betula papyrifera** Marsh.	WHBI
Wild red currant	**Ribes triste** Pall	WRCU
Wild red raspberry	**Rubus strigosus** Michx.	WRRA
Willow	**Salix** spp.	WILL
Bluejoint grass	**Calamagrostis canadensis** (Michv.) Beauv.	BJGR
Brome	**Bromus** spp.	BROM
Downy chess	**Bromus tectorum**	DOCH
Hairy wild rye	**Elymus innovatus** Beal	HWRY
Sedge	**Carex** spp.	SEDG
Western wheat grass	**Agropyron smithii** Rydb.	WWGR
Arrow-leaved coltsfoot	**Petasites sagittatus** (Pursh) A.Gray	ALCO
Aster	**Aster** spp.	ASTE
Baneberry	**Actaea rubra** (Ait.) Willd	BABE
Blueberry	**Vaccinium myrtilloides** Michx	BLBE
Bishops cap	**Mitella nuda** L.	BICA
Bog orchid	**Habenaria** spp.	BOOR
Bunchberry	**Cornus canadensis** L.	BUBE
Coltsfoot	**Petasites palmatus** (Ait.) A. Gray	COFO
Common horsetail	**Equisetum arvense** L.	COHO
Common pink wintergreen	**Pyrola asarifolia** Michx.	CPWI
Common yarrow	**Achillea millefolium** L.	COYA
Cow parsnip	**Heracleum lanatum** Michx.	COPA
Common dandelion	**Taraxacum officinale** Weber	CODA
Dewberry	**Rubus pubescens** Raf.	DEBE
Fairy-bells	**Disporum** spp.	FABE
Fireweed	**Epilobium angustifolium** L.	FIWE
Goldenrod	**Solidago** spp.	GORO
Horsetail	**Equisetum pratense** Ehrh.	HORS
Indian paint-brush	**Castilleja** spp.	IPBR

Continued

APPENDIX II (Continued).

Common Name	Scientific Name	Code
Lily-of-the-valley	**Maianthemum canadense** Desf.	LOVA
Marsh marigold	**Caltha palustris** L.	MAMA
Moose-ear chickweed	**Cerastium arvense** (L.)	MECH
Northern bedstraw	**Galium boreale** L.	NOBE
Oak fern	**Gymnocarpium dryopteris** (L.) Newn.	OAFE
Pea vine	**Lathyrus ochroleucus** Hook.	PEVI
Pineapple-weed	**Matricaria matricarioides** Less.) Porter	PIWE
Showy aster	**Aster conspicuus** Lindl.	SHAS
Star-flowered Solomon's seal	**Smilacina stellata** (L.) Desf.	SFSS
Striped coral-root	**Corallorhiza striata** Lindl.	STCR
Sweet-scented bedstraw	**Galium triflorum** Michx.	SSBE
Tall lungwort	**Mertensia paniculata** (Ait.) G. Don	TALU
Twin-flower	**Linnaea borealis** L.	TWFL
Veiny meadow rue	**Thalictrum venulosom** Trel	VMRU
Violet	**Viola** spp.	VIOL
Water avens	**Geum rivale** L.	WAAV
Western clematis	**Clematis verticellaris** Nutt.	WECL
White meadowsweet	**Spiraea lucida** Dougl.	WMSW
Wild mint	**Mentha** spp.	WIMI
Wild sarsaparilla	**Aralia nudicaulis** L.	WISA
Wild strawberry	**Fragaria virginiana** Duchesne	WIST
Wild vetch	**Vicia americana** Muhl.	WIVE
Woodland horsetail	**Equisetum sylvaticum** L.	WOHO
Yellow avens	**Geum macrophyllum** Willd.	YEAV

Appendix III. Forb biomass (kg/ha) by age class in the Medicine Lake study area, 1981.

Forb Species	Clearcut A	Clearcut B	14 yrs	30 yrs	60 yrs
Arrow-leaved coltsfoot				0.8	
Aster	66.0	24.3	6.1	129.7	26.8
Baneberry	1.2			11.9	
Blueberry		3.4	26.5	17.7	
Bishop's cap	4.3	0.2	1.7	11.6	15.4
Bog orchid			1.3		0.2
Bunchberry	20.3	22.1	6.0	18.5	16.2
Coltsfoot	19.7	4.5	12.1	26.7	7.2
Common horsetail	1.0		9.6	3.5	7.8
Common pink wintergreen	4.8	1.3	1.4	18.5	6.0
Common yarrow	0.3			94.3	
Cow parsnip				6.0	2.5
Common dandelion	5.5			0.6	
Dewberry	66.2	30.6	20.5	34.2	40.0
Fairybells					6.0
Fireweed	91.5	289.3	314.7	215.4	141.6
Goldenrod	1.0			1.7	17.2
Horsetail				5.8	4.0
Indian paint-brush			9.6		
Lily-of-the-valley	4.4	2.4	3.3	7.8	3.6
Marsh marigold			1.9	1.1	11.9
Moose-ear chickweed			5.5		0.2
Northern bedstraw	0.9	3.3	4.5	5.2	1.5
Oak fern	0.7			3.0	0.5
Pea vine	70.3	28.9	19.3	22.4	22.2
Pineapple weed		0.2			
Showy aster	54.6	0.3	90.2		34.6
Star-flowered Solomon's seal			0.5		
Striped coral-root				0.9	
Sweet-scented bedstraw	1.9	3.3	1.3	6.4	2.1
Tall lungwort	57.4	45.6	14.1	39.8	11.9
Twin-flower	1.7	2.2	0.9	8.5	13.9
Veiny meadow rue			91.9		
Violet	1.2			2.0	30.6
Water avens				1.1	
Western clematis	4.1		0.7	0.8	
White meadowsweet	11.1	24.9	7.7	99.8	
Wild mint		1.0	0.5		
Wild sarsaparilla	23.2	35.0	30.4	49.7	61.1
Wild strawberry	14.6	15.1	1.9	32.6	10.0
Wild vetch	8.4	3.5	13.0	2.4	2.3
Woodland horsetail	1.0	0.3	0.6	9.2	7.2
Yellow avens					17.2

Appendix IV. Grass and short woody shrub biomass (kg/ha) by age class in the Medicine Lake study area, 1981.

Species	Clearcut A	Clearcut B	14 yrs	30 yrs	60 yr
WOODY SHRUBS					
Aspen	92.1	16.0			
Balsam poplar	63.8	171.9		12.2	1.3
Bluefly honeysuckle					38.9
Bracted honeysuckle	49.8	119.7	24.8	1.1	32.8
Currant				3.6	
Green alder					
Low-bush cranberry	42.8	20.4	13.2	27.3	17.8
Red-osier dogwood	2.7		8.3		
Rose	57.3	79.5	43.3	40.3	28.6
Saskatoon					3.3
Snowberry	6.7	17.4	2.7	14.3	1.8
White birch	0.2		1.1		
Wild red currant	15.7			5.9	7.2
Wild red raspberry	138.5	61.0	36.4	12.6	33.8
Willow	0.3	4.5	0.3	9.1	
GRASSES					
Bluejoint grass	215.0	152.0	358.3	249.9	128.1
Brome	1.4		1.1		
Downy chess	5.6		33.6		1.3
Hairy wild rye			1.1		
Sedge	13.3		6.5		
Western wheat grass		0.5		13.0	1.0

APPENDIX V. Comparisons of habitat variables (% cover) by grid in the Medicine Lake study area.

Habitat Variable	Clearcut A		Clearcut B		Edge A		Edge B		14 A		14 B		14 C		30 A		30 B		60 A		60 B		80 A	
	%	S.E.	%	S.E.	%	S.E.	%	S.E.	%	S.E.	%	S.E.	%	S.E.	%	S.E.	%	S.E.	%	S.E.	%	S.E.	%	S.E.
CANOPY																								
Total Cover	0		0		13.8	8.7	31.4	21.0	1.7	4.6	3.4	9.9	23.7	13.6	31.7	13.9	41.6	21.2	32.8	19.3	33.6	18.6	19.9	13.2
Aspen	0		0		8.5	7.9	14.1	14.9	1.0	3.1	2.3	7.2	11.7	12.2	19.0	14.6	17.4	16.9	11.8	12.7	14.4	13.4	9.8	9.8
Balsam poplar	0		0		3.8	7.3	5.3	10.1	0.6	2.2	0.1	0.7	8.7	12.6	9.9	12.6	11.6	19.0	9.4	13.6	12.7	15.3	8.9	11.0
White birch	0		0		1.5	3.0	11.7	16.2	0		0.9	7.1	3.2	7.0	3.1	8.5	10.5	15.1	6.2	14.7	2.4	6.1	0.4	2.6
Conifers	0		0		0		0		0.1	0.6	0		0.1	1.0	0		2.2	5.2	5.3	12.8	4.1	12.0	0.8	4.1
TALL SHRUB																								
Total Cover	3.3	10.0	2.4	4.7	23.5	19.6	6.7	7.0	32.3	22.8	31.6	21.7	26.4	16.3	24.8	18.8	22.0	19.8	19.4	18.8	23.9	18.8	17.1	14.7
Aspen	0.8	2.1	0		0.9	1.6	0.2	0.8	8.5	9.6	7.3	10.9	1.1	3.9	0.2	0.8	0.6	1.8	0		0.3	1.3	0.1	0.7
Balsam poplar	1.1	5.9	1.5	3.8	1.2	3.0	0		2.9	5.3	6.1	11.2	0.5	1.4	0.3	0.9	0.7	1.6	0.7	2.1	0.8	3.2	1.1	2.1
White birch	0		0.9	3.3	0.5	1.9	3.3	3.9	2.2	8.1	1.5	4.0	0.3	1.0	1.1	2.6	1.8	4.7	3.6	6.6	1.4	2.4	1.6	3.5
Willow	1.3	5.2	0		4.8	6.9	1.9	5.4	8.2	13.8	7.3	10.2	12.7	15.2	7.0	10.3	6.6	7.7	3.6	7.4	2.2	4.8	0.1	0.1
Green alder	0.2	0.8	0		16.5	14.7	0.8	2.0	10.4	15.2	9.3	15.9	11.9	10.0	16.2	14.5	11.8	16.6	11.1	13.3	12.2	11.9	10.9	12.4
Conifers	0		0		0		0.3	0.9	0		0		0		0.1	0.6	0.6	1.5	0.4	3.1	6.9	8.6	3.4	8.8
LOW SHRUB																								
Total Cover	17.8	16.9	26.0	17.9	14.3	8.4	36.9	16.9	10.0	9.2	16.5	16.5	17.0	10.8	23.7	15.0	31.8	22.2	32.3	21.0	32.8	19.5	44.5	20.0
Aspen	7.7	11.8	11.0	10.5	1.3	2.9	2.0	5.2	0		0.6	2.3	0		0		0.1	0.7	0.1	0.6	0		0.5	1.2
Balsam poplar	3.3	5.2	4.3	8.7	0.6	2.0	3.5	7.9	0		0		0		0		0.1	0.6	0.3	0.9	0.1	0.1	0.7	1.2
White birch	0.1	0.5	1.5	4.3	0		0.8	1.6	0.8	0.6	0.1	0.5	0.1	0.4	0.2	0.6	0.4	1.2	0.7	2.0	0.4	1.0	0.3	1.0
Willow	3.1	3.3	0.2	0.7	0.9	1.4	0.3	0.8	0.2	0.7	3.8	10.9	1.5	3.1	0.3	0.8	2.1	3.3	1.0	2.1	0.2	0.6	0.2	0.8
Green alder	2.4	3.4	0.1	0.6	3.9	4.3	0.5	1.1	1.8	2.8	2.0	6.2	1.6	2.3	1.7	2.6	1.4	2.3	2.6	3.9	1.5	2.3	6.2	8.4
Low-bush cranberry	0		0.7	2.3	2.0	3.2	7.2	9.2	4.0	7.2	1.5	3.2	2.4	4.1	5.8	5.3	11.1	12.3	3.2	4.5	7.4	8.2	10.9	8.3
Rose	0.7	1.2	4.1	4.1	2.2	2.3	9.6	9.5	1.8	2.3	4.2	5.6	5.0	5.1	7.2	6.6	5.9	7.6	5.1	6.3	10.4	10.5	10.5	9.5
Bracted honeysuckle	0.2	0.8	2.0	4.6	2.4	5.8	4.6	4.6	1.6	2.5	0.6	1.4	3.6	4.7	5.1	7.6	7.6	9.0	14.7	12.2	9.7	10.1	11.3	12.7
Other species	0.4	1.2	2.0	2.6	1.0	1.5	8.6	9.9	0.5	0.9	3.6	7.4	2.8	3.3	3.4	6.6	2.8	4.3	4.5	6.5	4.0	4.5	4.0	3.8
GROUND LAYER																								
Bare soil	9.2	13.9	0.7	3.1	4.0	7.7	0.2	0.7	0		0		0		0		0		0.1	1.4	0		0	
Leaf litter	0		0		3.0	5.8	3.3	3.1	10.7	10.5	5.9	8.3	15.7	16.5	21.5	17.8	13.7	15.7	11.1	14.1	12.1	12.6	2.9	4.7
Water	1.7	7.0	0		1.3	6.5	0.9	5.3	0		0.7	3.7	0.2	0.8	0		0		0.1	0.6	0		0	
Monocots	42.6	26.0	67.0	19.9	35.0	27.6	31.6	22.8	32.7	25.9	32.7	22.3	30.0	27.0	20.2	22.2	4.5	4.5	20.4	21.9	17.8	20.2	27.3	22.0
Dicots	34.7	20.5	25.9	12.7	47.2	24.4	40.4	20.1	51.4	21.0	50.2	19.1	48.4	17.8	44.9	16.0	59.9	19.5	45.8	17.6	45.1	18.0	38.4	18.0
Horsetail	0.3	0.7	0		0.1	0.4	0.9	1.5	0.1	0.3	0.1	0.4	0.5	1.2	0.5	1.3	0.6	1.1	0.7	1.6	1.2	2.3	0.6	1.9
Moss	0		0		1.2	2.4	0.4	1.0	0.9	1.3	0.6	1.4	0.6	1.2	0.8	2.0	2.5	2.3	2.2	5.0	3.3	4.7	0.4	1.1
Lichen	0		0		0		0		0		0		0		0		0		0		0.1	0.6	0.8	0.1
CANOPY HEIGHT (m)	0		0		16.1	2.6	16.6	3.5	5.8	9.4	5.5	9.8	14.5	4.1	15.4	1.9	14.3	1.9	19.6	1.9	16.6	3.2	22.4	5.6
CANOPY DEPTH (m)	0		0		7.5	2.0	7.2	1.9	2.3	3.8	2.6	4.5	5.2	2.2	5.2	1.3	5.8	1.8	7.5	2.5	6.6	2.1	6.1	2.4
NUMBER OF PLOTS	75		23		29		43		66		72		120		120		102		120		120		120	

APPENDIX VI. Density of breeding bird territories recorded by study grid on the Medicine Lake study area.

Bird Species	Clearcut A				Clearcut B		14 A		14 B	30 A		30 B	30 C	60 A		60 B	80 A
	1981		1982		1982		1981	1982	1982	1981	1982	1982	1982	1981	1982	1982	1982
	Cut	Edge	Cut	Edge	Cut	Edge											
Goshawk														P*	P		
Broad-winged hawk										P	P			P	P		
Marsh hawk			P														
Ruffed grouse								P	P	P	P		P				
Killdeer	19.4		P														
Common snipe	19.4					P		P	P		P	P					
Spotted sandpiper			P														
Solitary sandpiper	19.4		P						P					P			
Mourning dove																	P
Ruby-throated hummingbird			P					P	16.2							P	
Common flicker				P											P		8.4
Pileated woodpecker						P		P	P								8.4
Yellow-bellied sapsucker			P														P
Hairy woodpecker			5.6	93.2		P		P	48.5	8.4	12.6	P					
Alder flycatcher		37.5		310.6			230.9	257.6	56.6	8.4	P			P	58.9	P	P
Least flycatcher								P	P								
Tree swallow		28.1				P	17.8	17.8	P	16.8	P	P	9.7	29.5	8.4	P	8.4
Black-capped chickadee																	P
Boreal chickadee		P				P	26.6	P		8.4	8.4			16.8	P	P	8.4
Red-breasted nuthatch		9.4		62.1				17.8	P								
House wren		18.7		62.1		P	17.8	P	P			4.2		P	P		P
American robin						P		P	8.1	8.4	P	8.4	P				
Hermit thrush				31.1				17.8	P	16.8	25.3	P	9.7	16.8	29.5	25.3	8.4
Swainson's thrush									P								
Mountain blackbird														8.4			
Golden-crowned kinglet															P		P
Ruby-crowned kinglet								P	P								
Cedar waxwing				P							P	P					P
Solitary vireo		28.1		124.2		28.4	26.6	35.5	64.7	33.7	50.5	29.5	19.4	37.9	33.7	16.8	12.6
Red-eyed vireo		9.4		62.1			26.6	35.5	16.2		8.4	8.4	9.7	4.2	8.4	8.4	8.4
Warbling vireo		18.7		P		P	26.6	26.6	32.3	16.8	16.8	16.8	4.9	16.8	16.8	8.4	
Black and white warbler		18.7		P		P	35.5	53.3	P	59.0	21.1	25.3	19.4	75.8	12.8	46.3	16.8
Tennessee warbler							P	17.8	8.1		P	P	P			4.2	
Orange-crowned warbler																	

Continued

APPENDIX VI. Continued.

Bird Species	Clearcut A				Clearcut B		14 A		14 B	30 A		30 B	30 C	60 A		60 B	80 A
	1981		1982		1982		1981	1982	1982	1981	1982	1982	1982	1981	1982	1982	1982
	Cut	Edge	Cut	Edge	Cut	Edge											
Yellow warbler							35.5	79.9	56.6								
Yellow-rumped warbler				62.1		P		17.8	P			8.4	19.4	4.2	8.4	12.6	12.6
Black-throated warbler						P							P	12.6	4.2		4.2
Blackpoll warbler		18.7															
Ovenbird		37.5		P		14.2				42.1	67.4	76.0	82.4	54.7	21.1	33.7	8.4
Connecticut warbler				P		56.8				8.4	4.2	4.2	P	P	P	P	P
Mourning warbler		65.5	22.5			14.2	17.6	P	32.3	25.3	21.1	33.7	9.7	42.1	46.3	P	33.7
Common yellowthroat									P								
American redstart		28.1		62.1			88.8	35.5	16.2	16.8	21.1	P	4.9	25.3	25.3	P	
Red-winged blackbird									P								
Northern oriole				P			17.8	P	P		P						P
Rusty blackbird								P	P								P
Brown-headed cowbird				62.1				17.8	P						P		
Western tanager				P				P							8.4		4.2
Rose-breasted grosbeak		28.1		62.1		P	17.8	35.5	16.2	8.4	8.4	8.4	9.7	8.4	8.4	P	8.4
Evening grosbeak				P											8.4		
Purple finch								P									
Pine siskin				P		P		P	P			P	P		P	P	P
American goldfinch			P					P	P								
LeConte's sparrow					73.0			P	P								
Dark-eyed junco		37.5	P	P		P	17.8	17.8	16.2	P	16.8	P	29.1	25.3	P	8.4	P
Chipping sparrow		84.3	11.3	124.2		85.2	17.8	8.9	P	16.8	16.8	16.8	43.6	33.7	25.3	58.9	42.1
Clay-colored sparrow			45.0		18.3			P	48.5	4.2	P						P
White-throated sparrow		103.0	11.3	155.3		14.2	124.4	62.2	48.5	54.7	29.5	33.7	9.7	101.0	54.7	25.3	50.5
Lincoln's sparrow	19.4		28.1		36.5				P	8.4	P						P
Song sparrow			P														
No. of Bird Species	4	16	6	13	3	6	16	17	15	18	15	13	14	17	17	11	16
Total Territories per 100 ha	77.6	572.3	123.8	1273.3	127.8	213.0	746.1	755.1	485.2	361.8	328.4	273.8	281.3	513.5	378.8	248.3	243.9
Grid Area (ha)	5.16	5.34	8.89	1.61	2.74	3.52	5.63	5.63	6.19	11.88	11.88	11.88	10.31	11.88	11.88	11.88	11.88
Species Diversity**	0.60	1.11	0.69	1.03	0.42	0.66	1.00	1.03	1.10	1.14	1.07	0.97	0.99	1.04	1.12	0.93	1.07

*P indicates the presence of a species whose territory was not mappable.

**Species diversity = $-\Sigma P_i \log P_i$

APPENDIX VII. Orientation of bird species to successional stages and special habitats of aspen forests.

	Herbaceous-Shrub (0–5 yrs)	Sapling (15–14 yrs)	Young (30 yrs)	Mature (60 yrs)	Overmature (80 yrs)	Intermittent Ponds	Grass-Forest Ecotone	Shrub-Forest Ecotone	Snags	Deadfall
Goshawk	F			●	●		F	F		
Broad-winged hawk			●	●						
Marsh hawk	●									
Ruffed Grouse		?	R	?	●		●	●		R
Killdeer	●					F				
Common snipe	●	F	F							
Spotted sandpiper		F				F	F			
Solitary sandpiper	●	●	●	●		F	●	●		
Mourning dove	●	R	R	R			●	R		
Ruby-throated hummingbird	F			●						
Common flicker	F	F	F	●	●		F	F	●	F
Pileated woodpecker				F	●				●	F
Yellow-bellied sapsucker		F	F	●	●		F		●	
Hairy woodpecker			F	●	●			F	●	F
Alder flycatcher	●	●	●		F	F	●	●		
Least flycatcher		●	●	●	F			●	F	
Tree swallow		F		R	R	F			R	
Black-capped chickadee		F	●	●	●		F	●	●	●
Boreal chickadee					●					
Red-breasted nuthatch		F	●	●	●		F	F	●	F
House wren	F	●	●	R	R			●	R	●
American robin	F	●	●	●	●		F	●		
Hermit thrush		●	●	F	F		F			●
Swainson's thrush		●	●	●	●			●		●
Mountain bluebird	F			R	R	F		●	R	●
Golden-crowned kinglet		F	F	●	●					
Ruby-crowned kinglet.			F	F	●		F	F		
Cedar waxwing		F	●	●	●					
Solitary vireo		●	●	●	●			F		
Red-eyed vireo	F	●	●	●	●		●	●		

R = Reproduction only

F = Feeding only

● = Reproduction and Feeding

Successional Stages

Special Habitats

APPENDIX VII. Continued.

	Herbaceous-Shrub (0-3 yrs)	Sapling (13-14 yrs)	Young (30 yrs)	Mature (60 yrs)	Overmature (80 yrs)	Intermittent Ponds	Grass-Forest Ecotone	Shrub-Forest Ecotone	Snags	Deadfall
Warbling vireo	F	●	●	●	●		F	●		
Black and white warbler		●	●	●			F	F		
Tennessee warbler		●	●	●	●		F	F		
Orange-crowned warbler		●	F	F			●	●		
Yellow warbler		●					●	●		
Yellow-rumped warbler		F	F	●	●		F	●		
Black-throated green warbler			F	●	●		F	F		
Blackpoll warbler								●		
Ovenbird			●	●	●		●	●		
Connecticut warbler			●	F	F		●	F		
Mourning warbler	●	●	●	●	●		●	●		
Common yellowthroat		F				F	F			
American redstart		●	●	●	●		F	F		
Red-winged blackbird		F					●	F		
Northern oriole		●	●	●	●		●	F		
Rusty blackbird		F			F					
Brown-headed cowbird	●	●	●	●	●			●		
Western tanager		F	F	●	●		●	●		
Rose-breasted grosbeak		●	●	●	●		F	●		
Evening grosbeak		F	F	●	●			F		
Purple finch	F	F	●	●	●		F	●		
Pine siskin	F	F	F	●	●		F	●		
American goldfinch	F	●	●	●	●		F	F		
LeConte's sparrow	●	F								
Dark-eyed junco	●	●	●	●	●		F	●		●
Chipping sparrow	●	●	●	●	●		●	●		●
Clay-colored sparrow	●	●			F					
White-throated sparrow	●	●	●	●	●		●	●		
Lincoln's sparrow	●	F	F		F		●	●		F
Song sparrow	F						●	●		●

R = Reproduction only

F = Feeding only

● = Reproduction and Feeding

Successional Stages

Special Habitats

APPENDIX VIII. Common and scientific names of birds referred to in this report.

Code	Common Name	Scientific Name
GOSH	Goshawk	Accipiter gentilis
BRHA	Broad-winged hawk	Buteo platypterus
MAHA	Marsh hawk	Circus cyaneus
RUGR	Ruffed grouse	Bonasa umbellus
KILL	Killdeer	Charadrius vociferus
COSN	Common snipe	Capella gallinago
SPSA	Spotted sandpiper	Actitis macularia
SOSA	Solitary sandpiper	Tringa solitaria
MODO	Mourning dove	Zenaida macroura
RUHU	Ruby-throated hummingbird	Archilochus colubris
COFL	Common flicker	Colaptes auratus
PIWO	Pileated woodpecker	Dryocopus pileatus
YESA	Yellow-bellied sapsucker	Sphyrapicus varius
HAWO	Hairy woodpecker	Dendrocopos villosus
ALFL	Alder flycatcher	Empidonax alnorum
LEFL	Least flycatcher	Empidonax minimus
TRSW	Tree swallow	Iridoprocne bicolor
BLCH	Black-capped chickadee	Parus atricapillus
BOCH	Boreal chickadee	Parus hudsonicus
RENU	Red-breasted nuthatch	Sitta canadensis
HOWR	House wren	Troglodytes aedon
AMRO	American robin	Turdus migratorius
HETH	Hermit thrush	Hylocichla guttata
SWTH	Swainson's thrush	Hylocichia ustulata
MOBL	Mountain bluebird	Sialia currucoides
GOKI	Golden-crowned kinglet	Regulus satrapa
RUKI	Ruby-crowned kinglet	Regulus calendula
CEWA	Cedar waxwing	Bombycilla cedrorum
SOVI	Solitary vireo	Vireo solitarius
REVI	Red-eyed vireo	Vireo olivaceus
WAVI	Warbling vireo	Vireo gilvus
BWWA	Black and white warbler	Mniotilta varia
TEWA	Tennessee warbler	Vermivora peregrina
ORWA	Orange-crowned warbler	Vermivora celata
YEWA	Yellow warbler	Dendroica petechia
YRWA	Yellow-rumped warbler	Dendroica coronata
BGWA	Black-throated green warbler	Dendroica virens
BLWA	Blackpoll warbler	Dendroica striata
OVEN	Ovenbird	Seiurus aurocapillus
COWA	Connecticut warbler	Oporornis agilis
MOWA	Mourning warbler	Oporornis philadelphia
COYE	Common yellow-throat	Geothlypis trichas
AMRE	American redstart	Setophaga ruticilla
NOOR	Northern oriole	Icterus galbula
REBL	Red-winged blackbird	Agelaius phoeniceus
RUBL	Rusty blackbird	Euphagus carolinus
BRCO	Brown-headed cowbird	Molothrus ater
WETA	Western tanager	Piranga ludoviciniana

Continued

Appendix III. Continued.

Code	Common Name	Scientific Name
ROGR	Rose-breasted grosbeak	Pheucticus ludovicianus
EVGR	Evening grosbeak	Hesperiphona vespertina
PUFI	Purple finch	Carpodacus purpureus
PISI	Pine siskin	Carduelis pinus
AMGO	American goldfinch	Carduelis tristis
LESP	LeConte's sparrow	Ammospiza leconteii
DAJU	Dark-eyed junco	Junco hyemalis
CHSP	Chipping sparrow	Spizella passerina
CLSP	Clay-colored sparrow	Spizella pallida
WHSP	White-throated sparrow	Zonotrichia albicollis
LISP	Lincoln's sparrow	Melospiza lincolnii
SOSP	Song sparrow	Melospiza melodia

APPENDIX IX. Use of cavities by wildlife species found in boreal aspen forests (adapted after Thomas 1979).

Species	Excavates cavity	Occupies cavity made by another species	Occupies "natural" cavities	Occupies space under loose bark	Construction part of courtship ritual	Nests and/or raises young	Roosting	Over-wintering	Hibernating
BIRDS									
Yellow-bellied sapsucker	●				●	●	●		
Downy woodpecker	●				●	●	●	●	
Hairy woodpecker	●				●	●	●	●	
Pileated woodpecker	●				●	●	●	●	
Black-backed three-toed woodpecker	●				●	●	●	●	
Northern three-toed woodpecker	●				●	●	●	●	
Black-capped chickadee	●	●	●			●	●	●	
Boreal chickadee	●	●	●			●	●	●	
White-breasted nuthatch	●	●				●	●	●	
Red-breasted nuthatch	●	●				●	●	●	
Tree swallow		●				●			
Brown creeper			●	●		●	●	●	
House wren		●	●			●			
Mountain bluebird		●	●			●	●		
Starling		●	●			●	●	●	
House sparrow		●	●			●	●		
American kestrel		●	●			●			
Boreal owl		●	●			●	●		
Hawk owl		●	●			●	●		
Pygmy owl		●	●			●	●	●	
Saw-whet owl		●	●			●	●	●	
Common flicker	●	●	●		●	●	●	●	
Common merganser			●			●			
Hooded merganser		●	●			●			

Types of Cavities | Uses of Cavities

APPENDIX IX Continued.

Species	Excavates cavity	Occupies cavity made by another species	Occupies "natural" cavities	Occupies space under loose bark	Construction part of courtship ritual	Nests and/or raises young	Roosting	Over-wintering	Hibernating
Bufflehead		●	●			●			
Wood duck		●	●			●			
Common goldeneye		●	●			●			
Barrow's goldeneye									
MAMMALS									
Deer mouse		●	●	●		●		●	
Short-tailed weasel		●	●			●			
Little brown bat		●	●	●		●	●	●	
Long-eared bat		●	●	●		●	●		
Hoary bat		●	●	●		●	●		
Silver-haired bat		●	●	●		●	●		●
Big brown bat		●	●	●		●	●	●	●
Red squirrel		●	●			●		●	
Northern flying squirrel		●	●			●		●	
Marten		●	●			●			
Fisher			●			●			

Types of Cavities / Uses of Cavities

POOR

QUALITY

ORIGINAL